

A KEY TO THE SPECIES OF
ACTORNITHOPHILUS FERRIS WITH NOTES
AND DESCRIPTIONS OF NEW SPECIES

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A KEY TO THE SPECIES OF *ACTORNITHOPHILUS* FERRIS WITH NOTES AND DESCRIPTIONS OF NEW SPECIES

By THERESA CLAY

SYNOPSIS

The characters of the genus *Actornithophilus*, its possible subgenera and the generic position of *Colpocephalum pediculoides* Mjöberg are discussed. Intra-specific variation and the characters which may be of phylogenetic and taxonomic importance are considered. A short account of the host-parasite relationships is given. The species, subspecies and local populations are discussed with special reference to the relation between size of the individuals in populations from related hosts. Notes are given on some of the species-groups comprising the genus ; seven new species are described and three neotypes and five lectotypes designated ; notes are given on the interpretation of some names. There is a key to the species, a glossary of terms used and a list of the species of *Actornithophilus* parasitic on the Charadriiformes.

INTRODUCTION

TIMMERMANN (1954 and 1957) has published a survey of the species of *Actornithophilus* in the British Museum (Natural History), and it has now been thought useful to publish a key for their identification.

The examination of a greater number of species and a better understanding of the characters of the Menoponidae has shown that "A Preliminary Key to the Genera of Menoponidae" (Clay, 1947) is unsatisfactory in a number of points, especially couplets 42-47 which include *Longimenopon* (referred to as "New genus F") and *Actornithophilus*. Emerson (1956) has rediscovered the interesting species *Colpocephalum pediculoides* Mjöberg, 1910, from the type host *Arenaria interpres* and since then Major W. W. A. Phillips has collected a good series from the same host in Ceylon, and recently some specimens from this host collected in Saudi Arabia have been found in the Meinertzhagen collection in the British Museum. Emerson discusses the generic position of this species and shows that it is somewhat intermediate between *Longimenopon* and *Actornithophilus* and decides on the characters of the head and the sparse abdominal chaetotaxy to place it in *Longimenopon*. The present writer, since examining better preserved material of *Longimenopon* and of *pediculoides* and comparing the latter with *Actornithophilus erinaceus* Timmermann (Text-fig. 13 and Timmermann, 1954, pl. 26, fig. b) and *A. sabulosus* sp. n. considers that the degree of the expansion of the head, the form of the pre-ocular notch and the density of the abdominal chaetotaxy, cannot be used as generic

characters in *Actornithophilus*. The characters of the dorso-lateral margin of the head and the position of the eyes in the available material of *Longimenopon* from the Procellariiformes appear to differ from those of *pediculoides* and of any of the species of *Actornithophilus*. The fact that *pediculoides* has a marked brush of setae on sternum IV, characteristic of *Actornithophilus* but not of *Longimenopon*, shows that this species, together with *sabulosus* sp. n., should be included in *Actornithophilus*. It may prove, however, that *Longimenopon* is not generically separable from *Actornithophilus* (see Timmermann, 1957 : 110). It is possible that these species with elongated heads and elongated, poorly sclerotized abdomens without well-marked pleural thickening and, in some species at least, extremely brittle setae, such as *Somaphantus lusus* Paine, *Longimenopon* spp., *Actornithophilus pediculoides* (Mjöberg) **comb. n.** and *Rediella mirabilis* Hopkins live inside the quill feathers. This would account for their rarity in collections and for certain characters which they have in common. *Somaphantus spencei* Emerson, which has the characters listed above, was found in the quill feathers of a peacock, and *Actornithophilus patellatus* (Piaget), also with these characters, lives in the quills of the curlew. Presumably their tubular form and soft and flexible abdomen is associated with having to pass through the hole which they make in the quill.

ACTORNITHOPHILUS Ferris, 1916

Actornithophilus Ferris, 1916. *Canad. Ent.* **48** : 303. Type species *Colpocephalum uniseriatum* Piaget.

Diactornithophilus Balát, 1953. *Zool. ent. Listy*, **2** : 96, 104. Type species : *Actornithophilus svobodai* Balát (= *svobodae* Balát).

Clypeodon Timmermann, 1954. *Ann. Mag. nat. Hist.* (12) **7** : 830. Type species : *Colpocephalum incisum* Piaget. **Syn. n.**

Menoponidae without sclerotized processes ("oral spines") arising near base of maxillary palpi and without combs of spine-like setae on the venter of the third femora or any of the abdominal sterna. Antennal fossae never deep; preocular notch present, never a narrow preocular slit; position of eyes normal; gular plate and setae present. Ends of temples square or flatly rounded. Pro-, meso-, and metasternal plates developed; two to three prosternal setae; mesosternal plate with one or more central setae. Mesothorax well defined dorsally with the four anterior mesothoracic setae not lying close together in one group, the outer seta each side is sometimes larger than the central ones (Text-fig. 16). Third femora and abdominal sternum IV with thick or sparse brushes, sterna III and V may also have brushes but always less well developed than those on IV. On abdominal tergites I-VIII the post-spiracular seta is the first seta at each end of the posterior marginal row.

At the present time it is difficult to suggest the affinities of many of the genera of the Menoponidae. In the case of *Actornithophilus*, all that can be said is that in the general characters of the head, the presence in some species of sexual dimorphism of the anterior setae of the head and in the sterna of the thorax, *Actornithophilus* resembles the *Colpocephalum* group; it differs in the arrangement of the anterior mesothoracic setae and the absence of combs of spine-like setae.

Species of *Actornithophilus* are known to parasitize representatives of all the families of the suborder Charadrii (*sens.* Peters, 1934) with the exception of the Jacanidae and Thinocoridae, and of all the suborder Lari with the exception of the Stercorariidae and Rynchopidae from which there are no authentic records. The only species (*A. perplanus*) taken from a member of the suborder Alcae was based on a single specimen and proves to belong to the *ochraceus* group; it was probably a straggler from *Pluvialis* or *Squatarola* (see below, p. 232). Timmermann (1954) has separated generically under *Clypeodon* the species *incisus* Piaget, *ceruleus* Timmermann and *pacificus* Timmermann, the latter name being a synonym of *incisus* (see below, p. 202). There is a possibility that both *incisus* and *ceruleus* are found on the Sterninae genus *Anous* (see below, p. 201). If this is the case the genus *Clypeodon* would be restricted to the species parasitizing this genus, while the species on the rest of the suborder Lari would be included in *Actornithophilus*. The *Clypeodon* group is distinguished by the sexually dimorphic setae of the head, an exaggeration of a character found in some species of *Actornithophilus* from the Charadrii, by differences in the male genitalia, the characters of which are not usually useful generic criteria, and by the sexual dimorphism in the shape of the head; on these characters the females are not generically separable. However, the characters given in the first couplet of the following key, common to the species found on the suborder Lari and serving to separate them from the species found on the Charadrii, may prove to be of greater phylogenetic importance. If this is the case then either the species from the Larinae and the rest of the Sterninae must also be included in *Clypeodon* or placed in another new genus, as they are more closely related to *Clypeodon* than they are to *Actornithophilus*, or alternatively all the species can be included in *Actornithophilus*. This latter solution will be adopted here.

Balát (1953) divided the species of *Actornithophilus* into two subgenera based on the chaetotaxy of the tergites, placing those with one or more rows of anterior setae in his new subgenus *Diactornithophilus*, type species *D. svobodai* Balát = *gracilis* Piaget from *Vanellus vanellus*. As shown below, the abdominal tergites of different specimens of one species may have no anterior setae, one or two on a segment, or a well-marked row, even within a population from one host individual. This division would also separate generically the *ochraceus* and *hoplopteri* groups which resemble each other in other characters. It does not therefore seem possible to recognize *Diactornithophilus* even as a subgenus.

VARIATION. It may be said at once that it is not possible to make a key which will identify every specimen of *Actornithophilus* correctly. Differences between species are largely based on chaetotaxy and there may be specimens which are abnormal in this character. An extreme example is a specimen found in a collection of *Actornithophilus* from *Vanellus vanellus* sent by Dr. Balát which is unlike any other known *Actornithophilus* in having the metanotum thickly covered with setae and extra setae on the dorsum of the temples; it differs from typical *gracilis* in having many more tergal setae. However, the form of the preocular nodi, the shape and size of the head and other characters suggest that this is a specimen of *gracilis* with abnormal chaetotaxy. In those species (example: *A. totani*) in which the

tergal chaetotaxy of the male is heavy, there may be considerable individual variation in the density of the anterior tergal setae. Specimens of *A. hoplopteri* s. l. usually have most of the tergites with some anterior setae, but within a given population there may be specimens with setae and others with none, and populations from some hosts rarely or never have anterior setae. Other examples are males of *sedes* and females of *uniseriatus* which may have no anterior tergal setae, a few, or a well-marked row on some tergites. The relative lengths of the post-spiracular setae may be useful taxonomic characters (Text-fig. 72), but show some individual variation; another useful taxonomic character is the presence or absence of anterior tergal setae on the last segment of the abdomen, but occasionally in the female a specimen may differ from the majority of the population in this character, for example one female of *limosae* has been found without these setae and one of *pustulosus* with them. Other characters which show individual variation are: (i) in the *ochraceus* group the relative lengths of dorsal head setae a and b and whether a is spiniform; (ii) the presence of a long central prosternal seta: this is always present in *patellatus* and *pediculoides* (Text-fig. 17) but in some species especially in the *umbrinus* group it is present only in an occasional specimen; (iii) the number and position of the ventral setae on the last segment of the male abdomen; (iv) the male genital sclerite which may show variation in the extent of the anterior division, although the junction of the sclerite to the sac may be a useful taxonomic character.

CHARACTERS OF PHYLOGENETIC AND TAXONOMIC IMPORTANCE. Keys, although useful as a method of delimiting populations into definable taxa and encouraging the study of individual variation in the search for constant specific characters, may give a false idea of relationships as useful key characters are not necessarily of phylogenetic importance (see also Bigelow, 1958). In *Actornithophilus*, in which the type of abdominal chaetotaxy gives such a distinctive appearance to the species and is useful taxonomically, the characters of possible phylogenetic importance may be overlooked. Thus, the populations from some species of *Tringa* resemble the rest of the *umbrinus* group from the Scolopacidae in the general appearance of the abdominal chaetotaxy while those from other species resemble some of the *hoplopteri* group from the Charadriidae. As it is the general rule for the Mallophaga parasitizing related¹ hosts to be themselves related, it seems reasonable to consider the characters common to populations from related hosts as ones of possible phylogenetic importance, although of course some of these may be directly adaptive and convergent in origin (see also Clay, 1951: 173). Balát (1953: 15) bases his subgenus *Diactornithophilus* on the number of rows of tergal setae, and thus includes the populations from *Vanellus*, *Tringa*, *Philomachus*, *Limosa*, *Calidris*; here also would have to go the populations from *Hoplopterus* and some other genera of the Vanellinae (sens. Peters, 1934). However, if the populations from this latter subfamily are considered together, a number of characters (see p. 202) can be found which are common to all the populations, and which separate them from the

¹ "Related" as applied to a group of taxa is used in the generally accepted sense that these taxa have a number of characters in common which separate them as a distinct group, whether or not some of the included taxa may actually be phylogenetically more closely related to other less similar taxa.

populations found on most of the Charadriinae (*sens.* Peters) and those from other host groups, and which are possibly less directly associated with the habitat provided by the feathers of the bird than is the abdominal chaetotaxy. Not all the host genera and species are parasitized by the species-group of *Actornithophilus* which would be expected from their generally accepted classification, but there are sufficient cases to make it possible to apply this method and to enumerate the characters which probably show relationship within the genus. These are: length of seta at base of labial palp, presence or absence of head sensillus 4 and dorsal head seta *d*, number of mesosternal setae (whether one or three or more), size of the preocular occipital and thoracic nodi, size of the marginal setae of the prothorax and metathorax (although there is a tendency towards individual variation here) and sometimes the form of the pleural thickening. Also sometimes the abdominal tergal chaetotaxy.

Characters which may be useful for the separation of species but do not necessarily show wider relationships are: the form of the dorso-lateral margin of the head; size of dorsal head setae *a*, *e* and *f*, and dorsal prothoracic seta *1*; the degree of development of the hypopharyngeal sclerite; the form of the prosternal plate and whether it surrounds the prosternal setae; the presence or absence of long anterior setae on the metanotum and anterior dorsal setae on the last abdominal segment; the number of tibial setae; the relative length and thickness of the post-spiracular setae; the setal pattern on the margins of the tergites; the number of rows and size of the anterior tergal setae; the number of inner posterior setae on the last segment of the female abdomen; the degree of development of the internal anterior processes of the tergites and the internal pleural thickening; and the form of the sclerite in the genital sac. The number and arrangement of the setae of the legs are fairly constant throughout the genus; differences are found in the size of the three setae at the distal end of the ventral surface of tibiae II–III, at least one of which is stout and spine-like, and in the number of setae along the outer lateral margins of tibiae I–III. On tibiae II and III there are usually two long and one or two short outer latero-ventral setae (Text-fig. 52), and a number of outer latero-dorsal setae, the two most distal of which are not included in the counts (Text-fig. 51). In *A. incisus*, *A. ceruleus*, *A. piceus* and *A. lari* the first outer latero-ventral seta is shorter and finer than in other species of *Actornithophilus* and in *A. tetralicis* sp. n. there are one to two extra latero-ventral setae (Text-fig. 54), and the outer latero-dorsal setae of tibiae II–III are more numerous. These differences may not always be obvious when the leg is distorted in some way during mounting. There are other minor characters which appear in the key, and of course there may be others which have been overlooked.

One of the most useful characters is the setal pattern on the margins of the tergites. Setal pattern A (see glossary) is found on the margin of the metathorax of all species from the Charadrii with the exception of most specimens of *grandiceps*, and on the abdominal tergites of certain groups. Even in those males in which there are more numerous marginal setae, there may be six stouter and longer setae which probably represent the six central setae of pattern A and in these species the females have setal pattern A, at least on tergite VIII; this suggests that it may be the primitive setal

pattern of *Actornithophilus*. In the species where the males have setal pattern A, the females usually have the modified pattern A.1 (see glossary) on tergite VIII. When considering the possible phylogenetic relationships within the genus, this setal pattern may be important (see also Timmermann, 1957). If pattern A is the more primitive one, from which the denser chaetotaxy has been developed more than once, it would explain the apparent similarity of certain species from unrelated hosts. Thus all the known populations parasitic on the Charadriidae (*sens.* Peters, 1934) have setal pattern A on segments I–VII. They are also characterized by the large size of the preocular, occipital and thoracic nodi. Rather similar species are found on the Recurvirostrinae, *Glareola* and *Pluvianus* (family Glareolidae) and *Chionis* (family Chionidae). Whereas both the species from *Pluvianus* (*A. hoplopteri sens. lat.*) and *Chionis* (*A. pauliani*) seem to be genuinely related to *A. hoplopteri* and are perhaps fairly recent acquisitions from another host, the species from the Recurvirostrinae differ in a number of characters (see below, p. 208) and their apparent similarity to the *ochraceus* group may merely be due to the retention of certain primitive characters. This also may be the case with the species *A. sedes* from *Glareola*.

HOST-PARASITE RELATIONSHIPS. In considering the phylogeny and host relationships of *Actornithophilus* it is important to bear in mind the possibility that there may have been natural straggling of a temporary nature, natural straggling followed by establishment on the new host, or contamination during collecting. The species of *Actornithophilus* are fast runners and often leave the dead host when this is handled. They appear also to leave the host during incubation. Thompson (1936 : 94) and Eichler (1946 : 5) give records of species being found on eggs of waders. On some waders *Actornithophilus* is rare and the absence of competition may have made the establishment of a straggling species easier. It is possible that species with the simple setal pattern could have established themselves on a new host, the more complicated setal pattern of the species found on the Erolinae, for instance, perhaps being a special adaptation to the feathers of the hosts. There is also the possibility that there may have been some hybridization between populations, especially those of the *ochraceus* group (perhaps made possible by the simple setal pattern) which might account for the variation within populations and the difficulty of their systematics. Hybridization in the Mallophaga is of course different from that between free-living geographical subspecies where hybridization takes place between adjacent subspecies which are the most nearly related, whereas in the Mallophaga the two forms come into contact due to fortuitous straggling between hosts which happen to be nesting in close proximity.

At the present time, the material from some host species is meagre, sometimes only a few specimens from one host individual, making it impossible to judge the amount of variation or the possibility of contamination or natural straggling. Host-parasite relations must therefore be evaluated with circumspection due to the difficulty of deciding which characters are of phylogenetic importance, and because of the possibility of secondary infestations followed by some divergence or even the possibility of hybridization between the original and immigrant population. Below (p. 200) is given a method by which it may sometimes be possible to distinguish

between true and apparent relationships of populations and to deduce cases of secondary infestations. Taking all these possibilities into account, it may be of interest to see how far distribution of *Actornithophilus* follows the classification of their hosts as arranged by Peters (1934) (see also Timmermann, 1957). The family Charadriidae are parasitized by species of the *ochraceus-hoplopteri* group. Within this family the genus *Vanellus* has a distinct species, while the rest of the subfamily Vanellinae are with two exceptions (see below) parasitized by populations which can all be included in *hoplopteri sens. lat.* The subfamily Charadriinae are all, with the exception of *Charadrius vociferus* (possibly a case of secondary infestation, see below, p. 200) parasitized by populations of *ochraceus sens. lat.*, although *C. hiaticula semipalmatus* has a second species belonging to the *pediculoides* group (p. 228). This supports Peters (1934) and the classification of Bock (1958 : 56) that all the genera of the Charadriidae form a related group with a gap between the Vanellinae *sens. Peters* and the Charadriinae ; and follows Bock's contention of the close relationship of the "genera" comprising the Charadriinae on one side and the Vanellinae on the other, but differs in suggesting that *Vanellus* is somewhat distinct from the rest of the Vanellinae. Also apparently genuinely related to the *ochraceus-hoplopteri* group are the populations from *Pluvianus* (Glareolidae) (possibly a secondary infestation, see below) and from *Chionis* (Chionidae) ; that from the Burhinidae, although distinct, has some similarity to the *hoplopteri* group and those from *Glareola* (Glareolidae) and the Recurvirostrinae are rather similar to the *ochraceus* group, but this may not be significant in terms of relationship (see above). The Scolopacidae are parasitized by members of the *umbrinus* group with the exception of *Arenaria* which has a distinct species and *Numenius arquatus* which has a quill-inhabiting species (see above, p. 192). The small amount of material from the Phalaropidae also belongs to the *umbrinus* group, but further confirmation that this is the true host is desirable. Within the *umbrinus* group, it does not seem possible at this stage to say which species are likely to be more closely related to each other with the exception of the related species on *Philomachus* and on the rest of the Erolinae. The *grandiceps* group found on *Haematopus* (Haematopodidae) and *Ibidorhyncha* (Recurvirostridae) is quite distinct from other species-groups ; the populations on the two hosts cannot satisfactorily be separated on present material. The Dromadidae and the Rostratulidae each have distinct species.

THE SPECIES, SUBSPECIES AND LOCAL POPULATIONS. These categories in the Mallophaga have been discussed elsewhere (Clay, 1958) with special reference to the ischnoceran genus *Degeeriella*. Johnson (1960) has also discussed the use of the subspecific category in the Mallophaga and Anoplura and suggests that as there is no information at present available on whether two populations can interbreed freely it is a purely subjective category and serves no useful purpose in the taxonomy of these groups. Although it seems that the subspecific category can be applied usefully, although arbitrarily, to some of the ischnoceran genera its application in the Amblycera is less satisfactory. Until more is known about the relationships between populations in this superfamily it is perhaps better not to make any use of the category.

In *Actornithophilus* there is the usual difficult and time-wasting problem of which

populations within a group of similar populations should be recognized nomenclatorially. In this genus, as in the majority of mallophagan genera where there are a number of related populations, those parasitizing the larger hosts tend to comprise larger individuals. Text-fig. 1 shows the relationship between the breadth of the head in the *ochraceus-hoplopteri* group and the wing length of their hosts. This can only be a rough approximation of the relation between size of host and parasite, as wing length is not always an index of general size. Also in most reference books only the observed range of wing measurements is given so it has been necessary to use Simpson's "crude mean" (1941), that is, the sum of the maximum and minimum measurements given divided by two. If there were available detailed measurements of feather parts of related species of birds which differ in size (see Rensch, quoted in Clay, 1951 : 209) it might be possible to make exact correlations between size of louse and size of host and perhaps to make more reliable and useful deductions. In the case of the parasite some of the populations are represented by rather small numbers (especially Nos. 1-4 and 7, Text-fig. 1), in a few cases single specimens, so that the exact position of the mark might be different if a larger number of measurements had been taken. But the diagram is sufficient to show the general association between size of host and parasite and also demonstrates how a population which does not fit into the general trend of such an association stands out and its true status can be given further consideration. Examples of such populations are those from *Pluvianus*, *Charadrius vociferus* and *Burhinus*. The populations from *Pluvianus aegyptius* (No. 5) cannot satisfactorily be separated morphologically from *A. hoplopteri* although the preocular nodus¹ is relatively smaller (Text-fig. 36). The individuals average larger than would be expected from the size of the host, but this discrepancy may partly be due to the fact that *Pluvianus* has rather shorter wings in relation to its body size than the species of *Charadrius* shown in the diagram. This relation between wing length and body size must always be considered when comparing host-parasite ratios. Even taking this into account, the average size of parasites is perhaps still larger than would be expected. *Pluvianus*, included in the Glareolidae by Peters (1934) is not considered to be related to the Vanellinae, to which the hosts of *hoplopteri* mostly belong, and the fact that it is parasitized by a population of this latter species, of which the individuals are larger than would be expected from the size of the bird, suggests the possibility that it is a rather recent acquisition from one of the African Vanellinae which are larger than *Pluvianus*.

The parasites of *Charadrius vociferus*, unlike those of all other known species of *Charadrius*, belong to *A. hoplopteri sens. lat.* They are the smallest in size of all known populations of *hoplopteri*, as would be expected from the size of the host, and relatively smaller than members of *ochraceus* from other species of *Charadrius*, but it is possible that the host-parasite size ratio of *ochraceus* and *hoplopteri* are different (there is a suggestion of this in the diagram). *A. hoplopteri* is probably found on *C. v. vociferus* throughout its range; specimens have been seen from British Columbia, Utah, Oklahoma, Texas and California. This, together with the host-parasite size ratio, suggests that if this is a case of secondary infestation the parasite must have been established on this host early in its history. The parasites of

¹ The exact shape of the preocular nodus is not of diagnostic value as there may be individual variation.

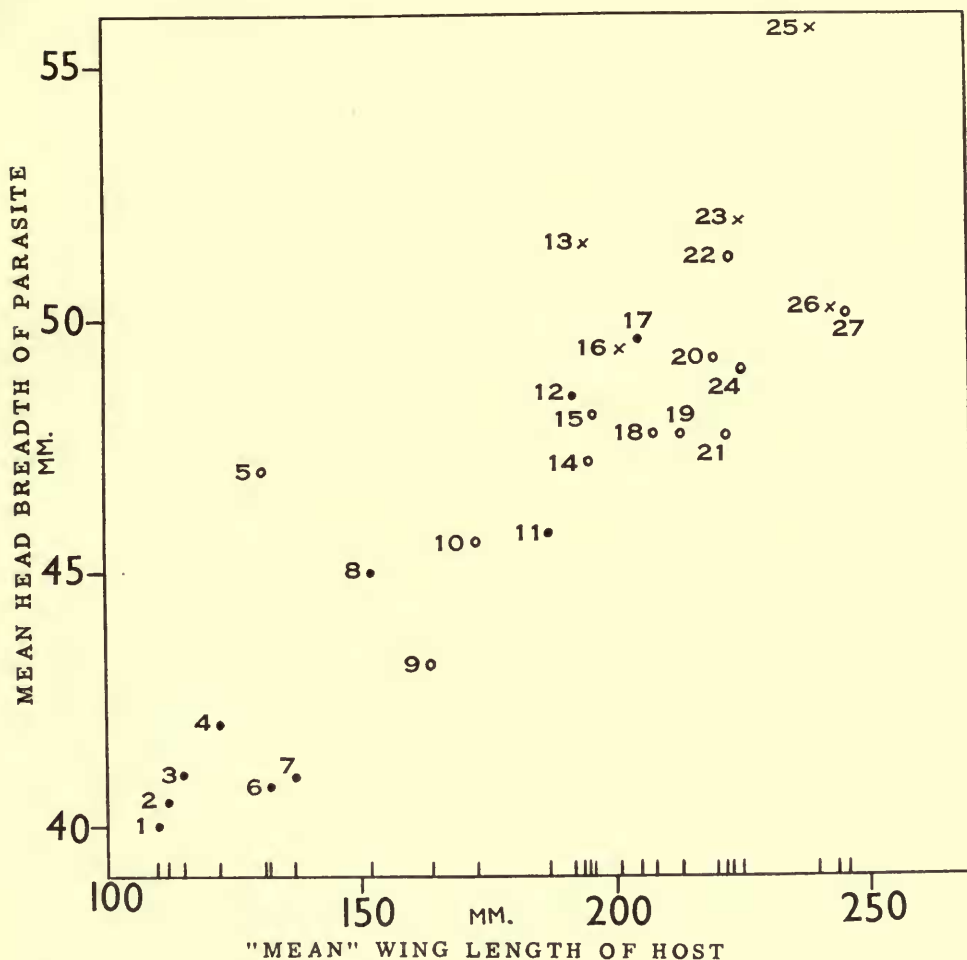


FIG. 1. Diagram illustrating relation between size of parasite and size of host. Numbers 1-27 host species (names according to Peters, 1934): 1. *Charadrius tricoloris*. 2. *Charadrius alexandrinus*. 3. *Charadrius dubius*. 4. *Charadrius mongolus*. 5. *Pluvianus aegyptius*. 6. *Charadrius hiaticula*. 7. *Charadrius leschenaultii*. 8. *Eudromias morinellus*. 9. *Charadrius vociferus*. 10. *Chettusia leucura*. 11. *Pluvialis apricaria*. 12. *Squatarola squatarola*. 13. *Glareola pratincola*. 14. *Hoplopterus duvaucelii*. 15. *Hoplopterus spinosus*. 16. *Stephanibyx coronatus*. 17. *Chettusia gregaria*. 18. *Hoplopterus armatus*. 19. *Xiphioidopterus albiceps*. 20. *Stephanibyx melanopterus*. 21. *Lobivanellus indicus*. 22. *Ptiloscelys resplendens*. 23. *Vanellus vanellus*. 24. *Afribyx senegallus*. 25. *Burhinus oedicnemus*. 26. *Chionis minor*. 27. *Lobibyx novaehollandiae*. ●—*Actornithophilus ochraceus* sens. lat. ○—*A. hoplopteri* sens. lat. ×—Other species of *Actornithophilus*. (Too many deductions should not be made from this diagram, see text.)

Burhinus (not included in the Charadriidae) average considerably larger than those from the Vanellinae and although similar to those of the *hoplopteri* group differ in a number of small characters, one of which is the size of the preocular nodi. In the *ochraceus-hoplopteri* groups this nodus either tends to increase in size with the size of the head, or remain relatively the same size, but in the population from *Burhinus* it is smaller than in some of the populations of *hoplopteri*, the heads of which average smaller (Text-figs. 33-40). These examples, even taking into account the unsatisfactory method of compiling the diagram, are sufficient to show that such diagrams may be used to bring to notice populations which are in some way anomalous and may either belong to distinct or not closely related species or be due to secondary infestation. It is possible to follow the character gradients and any population in which a character goes against the general trend of association with size of the parasite can be considered as being genetically more remote and should be examined for other character differences, as in the case of *A. tetracis* sp. n. from *Burhinus*. Such a diagram may also be used to check whether specimens taken from a given host are likely to belong to the established population or to be temporary stragglers. Specimens from *Chettusia gregaria* (Text-figs. 1, 17), for instance, unlike those from *C. leucura* and most of the rest of the Vanellinae, belong to the species *A. ochraceus*. They are, however, larger (as is the host) than those from any of the Charadriinae, but fit into the general host-parasite size ratio of *ochraceus*. This suggests that these specimens are the established parasite of *C. leucura* and (if the population is the result of secondary infestation) that they have been established for a sufficient length of time to become adapted to their new host.

As in the *ochraceus-hoplopteri* groups the populations of *umbrinus* (see p. 210) show a relationship between the size of the parasite and that of the host; correlated with these size differences are differences in the shape of the head and chaetotaxy of the abdomen, but if the populations from many hosts are compared it is found to be impossible to separate them satisfactorily into taxonomic units. Elsewhere (Clay, in press) it has been suggested that when a number of populations are included under one name it is useful to show this by the addition of the term *sensu lato*. This added to the specific or subspecific name indicates that the specimens are from a population belonging to this taxon, restricted to a definite host form or forms and presumably with a distinct gene complex. The population may be separable from that from the type host of the taxon only statistically or there may be other populations showing intermediate characters making nomenclatorial recognition unsatisfactory. In the case of some of these populations future work may reveal valid characters for separation.

NOTE ON MEASUREMENTS

Measurements of total length and of breadth and length of the abdomen are unreliable in many of the Menoponidae as they are dependent on the amount of pressure exerted by the cover slip in mounting. These measurements are given for one individual in the case of the new species as a general indication of size. The length of the head is again an unreliable measurement owing to the fact that the head often does not lie flat under the cover slip and the occipital margin may be

distorted. The measurements least affected by distortion seem to be those of the breadth of the head at the temples (B.1) and at the preocular enlargement (B.2) and probably the breadth of the prothorax. Owing to the difficulty of finding measurable examples of post-spiracular setae the numbers on which Text-fig. 72 is based are small, but these reflect the differences between the relative lengths of the post-spiracular setae in the species represented. All specimens measured are mounted in Canada balsam.

TAXONOMIC NOTES AND DESCRIPTIONS OF NEW SPECIES

The *piceus* Species-group

The populations of *Actornithophilus* found on the Laridae have not been revised in detail, and must wait for a larger amount of material from more host species. In general, individuals from the Sterninae (i.e. *piceus* Denny) are smaller than those from the Larinae (i.e. *lari* Packard) :

Breadth at temples in mm.		
	♂	♀
<i>piceus</i>	0.61-0.67	0.67-0.73
<i>lari</i>	0.71-0.74	0.77-0.80

However, the measurements of one male out of nine taken from an individual of *Larus fuscus* fall within the range of those of typical *piceus* (b.1, for instance, is 0.65 mm.) and does not seem to be separable. Piaget's type of *A. fuscipes* (host : *Larus dominicanus*), a female, measures 0.76 mm. and a single female from *Gelochelidon nilotica* measures 0.77 mm., but the host record needs confirmation. No specimens have been seen from the smaller gulls and it may prove that there is no way of separating the populations from the different divisions of the Laridae ; they are here all included under the name *A. piceus* (Denny), *sens. lat.* Only one male has been seen from *Gygis alba* and the measurement of this specimen and those given for the female holotype of *A. candidus* Carriker, 1949, fall within the range of measurements given above for *piceus* ; the male from *Gygis* has a greater number of abdominal tergal setae especially on segment II, but without further material it is not possible to say whether this is individual variation or not. It seems from the description of *candida* that this may have been based on a teneral female.

Lectotype of *Colpocephalum piceum* Denny: ♀ (slide No. 1) in the Denny collection, British Museum (Natural History).

***Actornithophilus ceruleus* (Timmermann, 1954)**

A. ceruleus was described from five specimens taken from skins of two forms of *Procelsterna cerulea*. Three ♂, 1 ♀ from skins of *Anous minutus melanogenys* from the South Seas and 1 ♂, 1 ♀ (K. C. Emerson collection) from *Anous m. minutus* on Lolobau Island, Bismarck Archipelago appear to be inseparable from *A. ceruleus*. Although the specimens taken from skins without an exact locality must be treated

with some doubt it seems that the pair in the Emerson collection could not be the result of contamination between *Procelsterna* and *Anous* as according to Dr. H. G. Deignan of the United States National Museum the former genus is not known to occur in the Bismarck Archipelago. Therefore either *A. ceruleus* occurs on both *Procelsterna* and *Anous* or the host record of the type material is incorrect.

Actornithophilus pacificus (Timmermann, 1955)

This species was described from five specimens taken from skins of two species of *Puffinus* from three localities; the specimens are in poor condition but appear to be the same as *A. incisus* from *Anous stolidus*. Unless further material of this species is found to occur naturally on *Puffinus* it must be assumed that the type material originated from *Anous*.

The *ochraceus* and *hoplopteri* Species-groups

The species of these two groups have the following characters in common: the large size of the preocular, occipital and thoracic nodi, a tendency in the males to have dorsal head seta *a* spine-like (Text-fig. 4); marginal prothoracic seta 5 and metathoracic seta 2 short and fine, although in the occasional specimen these setae may be longer; tergites with well-developed internal anterior processes (Text-figs. 55 and 56); tergites I–VII with setal pattern A and VIII with pattern A.1; last segment in both sexes without dorsal anterior setae; post-spiracular setae V and usually III markedly shorter than II and IV. The males of the *hoplopteri* group can at once be distinguished by the form of the sclerite in the genital sac (Pl. 7, fig. 5). Other characters distinguishing the species of the two groups are the shape of the preocular nodus which usually has a straighter anterior margin in *hoplopteri* (but there is some variation), the longer somewhat finer tergal setae and the less well-marked colour pattern in *ochraceus*. *A. crinitus* sp. n. from *Stephanibyx coronatus* is somewhat intermediate between the two groups (see below). *A. gracilis* from *Vanellus vanellus* is a well-marked form resembling the *ochraceus* group in the character of the male genital sclerite but differing from all other species of the two groups in the presence of long anterior metanotal setae. Morphologically *A. sedes* appears to belong to the *ochraceus* group (see also above, p. 196).

The populations comprising *A. ochraceus* (Nitzsch) *sens. lat.* are found on the subfamily Charadriinae (*sens. Peters*, 1934) with the exception of *Charadrius vociferus* (see p. 198). *Chettusia gregaria*, although belonging to the subfamily Vanellinae, is parasitized by *ochraceus* (see p. 200). As discussed above and shown in the diagram (Text-fig. 1) there is a general correlation between the size of the louse and the size of its host. Those lice with heads narrower across the temples have a tendency towards relatively longer heads and rather less elongated preocular nodi (Text-figs. 25 and 26), so that when comparing the extremes of size such as in populations from *Charadrius tricollaris* and *Squatarola squatarola* there is considerable difference in appearance of the individuals. However, examination of populations from other hosts show that these characters grade into each other and cannot be used for satisfactory taxonomic divisions. Dorsal seta *a* of the head of the male

may or may not be spiniform (Text-fig. 4), but it has been found that even within a population from one host form specimens are found with or without spiniform setae, sometimes differing on two sides of the head. Considerable variation is also found in the length of seta *a* relative to the length of seta *b*. In view of the variation and character gradients it seems more satisfactory to include all these populations under the name *ochraceus*. Thus the following described forms are considered to be synonyms of *A. ochraceus* (Nitzsch, 1818) *s. l.*:

A. flavipes (Giebel), *A. timidus* (Kellogg), *A. perplanus* (Kellogg & Chapman), *A. perrarus* Blagoveshtchensky, *A. laveni* Eichler, **syn. n.**

The *hoplopteri* group comprises *A. hoplopteri s. l.* and *A. pauliani*. Within *A. hoplopteri s. l.* the anterior tergal setae may be absent or show considerable variation in number. In most of the populations at least some of the tergites have one or more anterior setae and some segments have a definite row, but there may be individuals without anterior setae on any of the segments. In the populations from *Lobivanellus*, *Hemiparra* and *Hoplopterus duvaucelli* no individuals with anterior tergal setae have been seen, and in this way they resemble individuals of the *ochraceus* group. This is obviously a variable character and not always useful for specific separation.

A. hoplopteri s. l. is found on the Vanellinae with the exception of *Stephanibyx coronatus* which has a distinct species (see below) and *Chettusia gregaria*, already discussed above. It is also found on *Pluvianus* (discussed above, p. 198). The diagram (Text-fig. 1, 5) shows the general correlation between size of parasite and host. No characters have been found which would usefully separate any of these populations taxonomically.

The population from *Chionis minor*, recognized here as a species (*A. pauliani*), is near *hoplopteri* although the hosts are placed in different superfamilies. The parasites fit into the general trend for size in relation to size of host (Text-figs. 1, 26), but the preocular nodi are relatively smaller (Text-figs. 33, 39). *A. pauliani* also differs by the prosternal plate not surrounding the prosternal setae; the tergal setae being somewhat longer than in typical *hoplopteri* (Pl. 7, figs. 1, 2) and postspiracular seta III not being markedly shorter than IV (Text-fig. 72).

***Actornithophilus ochraceus* (Nitzsch, 1818)**

Type host : *Pluvialis apricaria* (Linn.)

(Pl. 9, fig. 2; Pl. 10, fig. 3; Text-figs. 2, 25–28, 55–56, 63)

The history and type host of this species has been discussed in Clay & Hopkins (1960 : 45). It is distinguished from other species from the Charadrii by the form of the preocular, occipital and thoracic nodi, form of the prosternal plate, form of the marginal setae of the thorax, absence of long setae on the metanotum, the tergal setal pattern of the metathorax and abdomen, the relative lengths of the postspiracular setae, absence of anterior setae on any of the tergites, the internal processes of the tergites and the sclerite of the genital sac. The female has tergal pattern A on segments I–VII and A.1 on segment VIII; there are no anterior

dorsal setae on the last segment and the posterior sternites are of the type shown in Text-fig. 71.

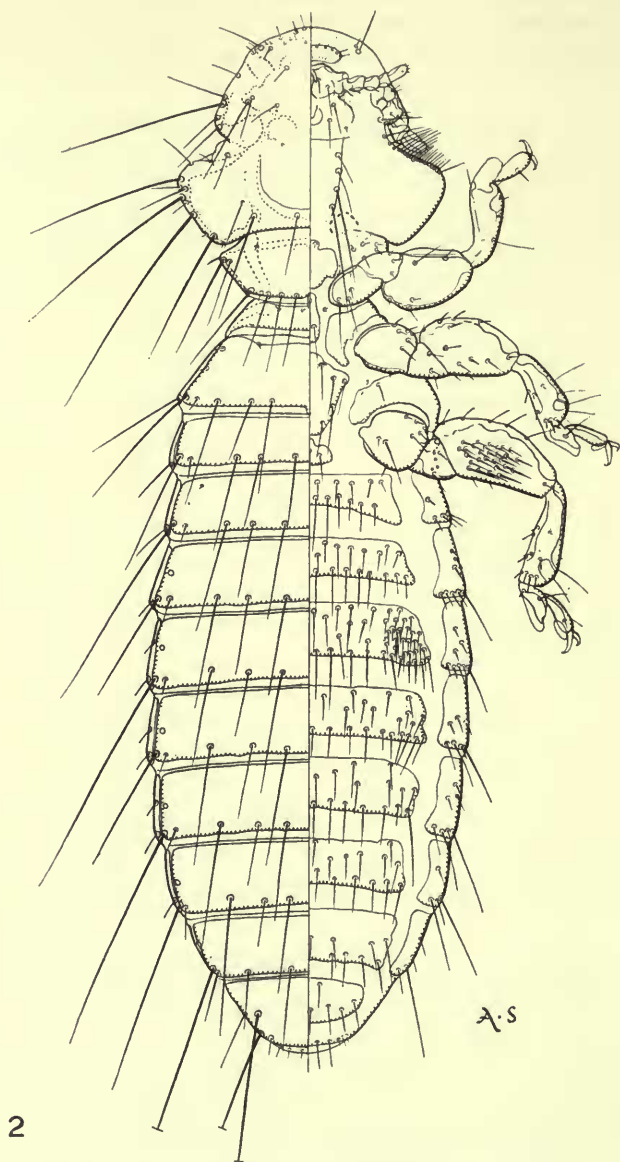


FIG. 2. *Actornithophilus ochraceus* (Nitzsch). Male from type host.

Neotype male and *neallotype* female of *Actornithophilus ochraceus* (Nitzsch, 1818) in the British Museum (Natural History), slide No. 16443a, from *Pluvialis apricaria* from Ireland, February, 1947.

Balát (1953 : 93) designated a male and a female as unofficial neotypes of this species ; however a neotype must be a single specimen so that it is necessary to re-designate the neotype before submitting an application to the International Commission on Zoological Nomenclature. Dr. Balát has most kindly presented to the British Museum (Natural History) the two specimens which he designated as neotypes. However, it has been decided not to use as neotype Dr. Balát's male specimen as this is exceptionally small for a specimen from *Pluvialis apricaria*. It is possible that the specimen is somewhat shrunk but even so its measurements fall within the range of those from the small species of *Charadrius* such as *C. hiaticula*. Dr. Balát says (in litt.) that there can be no doubt about the correct identification of the host as *apricaria* is the only species of *Charadrius* (sens. lat.) which comes to Czechoslovakia in December, the month in which the specimens were collected. It appears therefore that either these specimens of *Actornithophilus* are atypical or they are natural stragglers on the *apricarius* individuals from which they were collected. In either case they do not seem suitable type material and a specimen which is typical of the population from *Pluvialis* from various localities and which had already been drawn has been chosen as neotype.

Measurements in mm. of A. ochraceus from Pluvialis apricaria

	Male		Female	
	Length	Breadth	Length	Breadth
Head B.1	0.35	0.47	0.37	0.52
B.2	—	0.35	—	0.37
Prothorax	—	0.32	—	0.34
Metathorax	—	0.43	—	0.48
Abdomen	1.13	0.57	1.31	0.67
Total	1.78	—	2.00	—

Actornithophilus crinitus sp. n.

Type host : *Stephanibyx c. coronatus* (Boddaert)

(Pl. 4, fig. 1, Pl. 10, fig. 4 ; Text-figs. 4, 38, 50, 51, 52, 71)

This species is distinguished from all other species of *Actornithophilus* by the presence of at least three setae on both preocular enlargements. In general appearance it resembles *hoplopteri* from which it is separated by the characters of the prosternal plate and the sclerite of the genital sac, in addition to the head setae. If the type of genital sac (Pl. 10, fig. 3) found in *ochraceus* and other species of *Actornithophilus* is the more primitive form and therefore not of great phylogenetic importance, then it is probable that the affinities of *crinitus* lie with the *hoplopteri* group which it resembles closely in most of its characters ; the occasional specimen of *hoplopteri* and *ochraceus* may have three setae on the preocular enlargement on one side of the head.

MALE AND FEMALE. Male as shown in Pl. 4, fig. 1. The anterior margin of the preocular nodus is of the *ochraceus* type (Text-fig. 38); preocular enlargement with three or four setae each side (Text-fig. 4); dorsal head setae *a* spiniform in the male. The prosternal plate does not surround the prosternal setae and there are no long anterior setae on the metanotum. Form of the marginal setae on the prothorax, marginal tergal setal pattern of metathorax and abdomen, the relative lengths of the post-spiracular setae, internal processes of the tergites and the sclerite of the genital sac as in *ochraceus*. There are anterior setae on at least some of the abdominal tergites, and in all the females examined and most of the males some of the tergites (a greater number of these in the female than in the male) have a definite row of anterior setae. Length and thickness of tergal setae as in *hoplopteri*. There are no anterior setae on the tergite of the last segment. Genital region of female as in Text-fig. 71.

MATERIAL EXAMINED. 27 ♂, 32 ♀ from *Stephanibyx coronatus* (10 individuals) from Kenya, S.W. Africa and S. Africa.

Holotype male and *allotype* female, slide No. 20445 in the British Museum (Natural History) from *Stephanibyx c. coronatus* (Boddaert) from Isiolo, Kenya, January, 1956. *Paratypes*: 26 ♂, 31 ♀ with data as given above.

Measurements in mm.

	Male		Female	
	Length	Breadth	Length	Breadth
Head .	0.37	0.51	0.35	0.52
Prothorax .	—	0.33	—	0.34
Metathorax .	—	0.46	—	0.48
Abdomen .	1.15	0.55	1.35	0.67
Total .	1.85	—	2.05	—

Male breadth of head, b.1: range 0.48–0.51, mean 0.49; b.2: range 0.35–0.37, mean, 0.36 (10 specimens).

The *tetralicis* Species-group

This group is represented by a single species, *A. tetralicis* sp. n., the affinities of which are doubtful. The characters in which it resembles the *ochraceus-hoplopteri* group, that is, the spiniform setae of the male, marginal setae of the prothorax, metathorax and abdominal tergites may be primitive characters and of no phylogenetic importance. However, the sclerite of the genital sac appears similar to that of *hoplopteri* and may indicate relationship.

Actornithophilus tetralicis sp. n.

Type host: *Burhinus oedicnemus* (Linn.)

(Pl. 4, fig. 2, Pl. 9, fig. 5, Pl. 10, fig. 6; Text-figs. 22, 40, 48, 53, 54, 58)

This species is distinguished from the *ochraceus-hoplopteri* group by the relatively smaller preocular nodi (see above, p. 200), the more numerous setae on the legs and



3

FIG. 3. *Actornithophilus totani* (Schrank). Male from type host.

in the sternal brush, the relative lengths of the post-spiracular setae and the sclerite of the genital sac.

MALE AND FEMALE. Male as shown in Pl. 4, fig. 2. Preocular nodi as in Text-fig. 40; dorsal head setae a. spiniform in the male; prosternal plate surrounds prosternal setae. Marginal setal pattern of pronotum, metanotum and abdominal tergites as in *ochraceus*, relative lengths of tergal setae as shown in Text-fig. 48; post-spiracular setae III and V not markedly shorter than II and IV. Brushes on third femora and sternite IV thicker than in *ochraceus* and *hoplopteri* (Pl. 9, fig. 5). The chaetotaxy of the legs differs from most of the species from the Charadrii examined in having one or two extra outer latero-ventral setae on tibiae II-III and usually having more numerous latero-dorsal setae on tibiae I-III, III has 7-9 in the male and 7-10 in the female (see above, p. 195, Text-figs. 53-54). Sclerite in genital sac as in Pl. 10, fig. 6. Last segment of female abdomen as in Text-fig. 58. Measurements as given below. Specimens from Suffolk birds measure rather less than those from Israel, but this may partly be due to the condition of the Suffolk specimens.

MATERIAL EXAMINED. 6 ♂, 10 ♀ from *Burhinus oedicnemus* (Linn.) from Israel; 3 ♂, 11 ♀ from *B. o. oedicnemus* from Suffolk, England; 1 ♂ from *Burhinus s. senegalensis* (Swainson) from North Cameroon. 2 ♂, 3 ♀ in rather poor condition from *Esacus recurvirostris* (Cuvier) from Upper Burma may belong to this species.

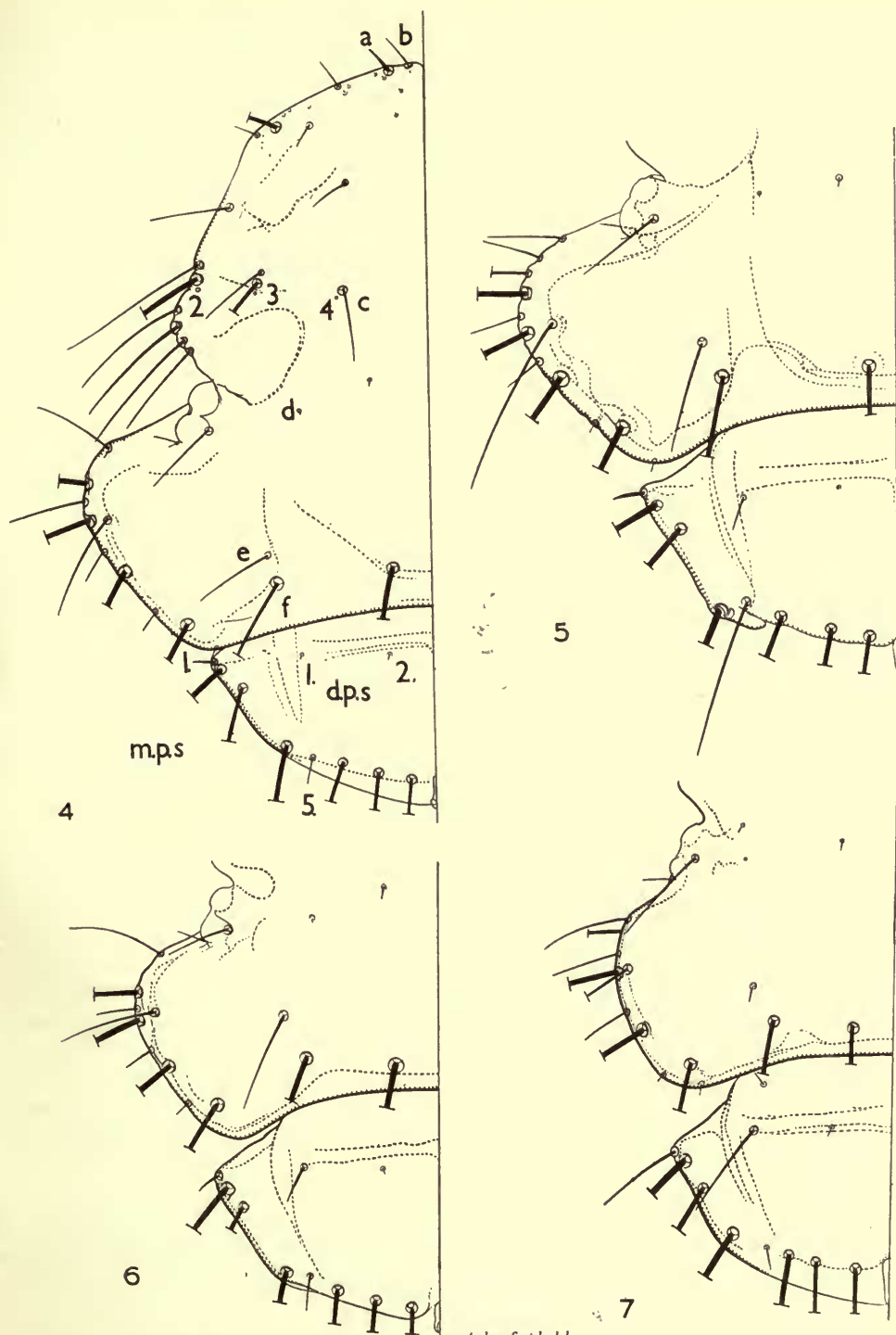
Holotype ♂ and *allotype* ♀ in the British Museum (Natural History) from *Burhinus oedicnemus* from Oranim, Israel collected by M. Costa, 20.v.1956. *Paratypes*: 2 ♂, 4 ♀ from the same host individual as the holotype and 3 ♂, 11 ♀ from the same host species from England, data as given above.

Measurements in mm.

	Male		Female	
	Length	Breadth	Length	Breadth
Head .	0.400	0.585	0.430	0.630
Prothorax .	—	0.380	—	0.410
Metathorax .	—	0.525	—	0.585
Abdomen .	1.380	0.710	1.630	1.030
Total .	2.185	—	2.530	—

The *uniseriatus* Group

The species comprising this group resemble those of the *ochraceus* group and should perhaps be included in it; they differ mainly in the characters of the chaetotaxy. Marginal prothoracic seta 5 and marginal metathoracic seta 2 (Text-figs. 5, 46) are usually longer and less fine than in *ochraceus* although in *mexicanus* the difference is less marked; the inner tergocentral setae of the abdomen are markedly shorter than the outer one each side (Text-fig. 49) and there is a tendency to have a greater number of tergocentral setae. Both sexes of *A. uniseriatus* and *A. mexicanus* usually have two or more segments with eight or more tergocentral setae, although occasional males are found in which the majority of tergites have six setae with one



Arthur Smith del.

FIGS. 4-7. Male head and prothorax (dorsal) of *Actornithophilus* spp. 4. *A. crinitus* sp. n. 5. *A. uniseriatus*. 6. *A. umbrinus*. 7. *A. sabulosus* sp. n. a-f.—dorsal head setae; 2-4.—dorsal head sensilli; m.p.s.—marginal prothoracic setae; d.p.s.—dorsal prothoracic setae.

or two having seven. In *A. himantopi* only an occasional female has one or two segments with eight tergoventral setae, the majority of males and females having tergal pattern A. Anterior setae on the tergites usually absent, only one specimen (a female of *A. uniseriatus*) has been seen with anterior tergal setae, and on two segments these form a definite anterior row. The sclerite in the genital sac is elongate and, allowing for individual variation, rather less deeply divided anteriorly than in *ochraceus*. *A. mexicanus* differs from the other two species in the male by having dorsal head setae a spiniform. The preocular nodi are similar to those of the *ochraceus* group and as in that group become shorter (from side to side) and broader (anterior-posteriorly) as the head decreases in breadth (Text-figs. 30-32).

It has not been possible to find any characters which can be used to separate the populations from *Recurvirostra avosetta* and *R. americana*, although in the small number of specimens available, the head breadth of the male in the population on *R. avosetta* averages larger than in those on *A. americana* :

R. avosetta population : range, 0.540-0.555 ; mean, 0.547 mm. (5) ;

R. americana population : range, 0.505-0.540 ; mean, 0.520 mm. (7).

A. uniformis (Kellogg) **syn. n.** is here considered as a synonym of *uniseriatus*.

Included species : *A. uniseriatus* (Piaget, 1880) ; *A. himantopi* (Blagoveshtchensky, 1951) and *A. mexicanus* Emerson, 1953.

The type series of *A. uniseriatus* in the Piaget collection of the British Museum (Natural History) comprises 1 ♂, 4 ♀, of which the male and one female on slide 1380 are *A. totani* and the remaining female on slide 1380 and the two females on slides 1382 and 1381 are the species usually found on *Recurvirostra avosetta*. In Clay (1953 : 657) the male was wrongly designated as lectotype ; this mistake is here rectified.

Lectotype of *Colpocephalum uniseratum* Piaget, 1880 : ♀ in the Piaget collection, British Museum (Natural History), slide No. 1380.

The *umbrinus* group

The *umbrinus* group is used here to include a number of species in which the preocular, occipital and thoracic nodi are small, the anterior head setae are not sexually dimorphic, the males usually do not have tergal setal pattern A, some tergites in both sexes have anterior setae, often numerous in the male, tergite VIII of the female normally has six or more central setae and the pleurites are not deeply bilobed as in the *ochraceus-hoplopteri* group. The species are found generally throughout the family Scolopacidae (*sens.* Peters, 1934), but *patellatus* from *Numenius arquatus* (see above, p. 192) and *bicolor* from *Arenaria*, of the subfamily Arenariinae, are not typical of the *umbrinus* group. The small amount of material said to have been taken from *Steganopus* (family Phalaropidae) can be included here but the host records need confirmation.

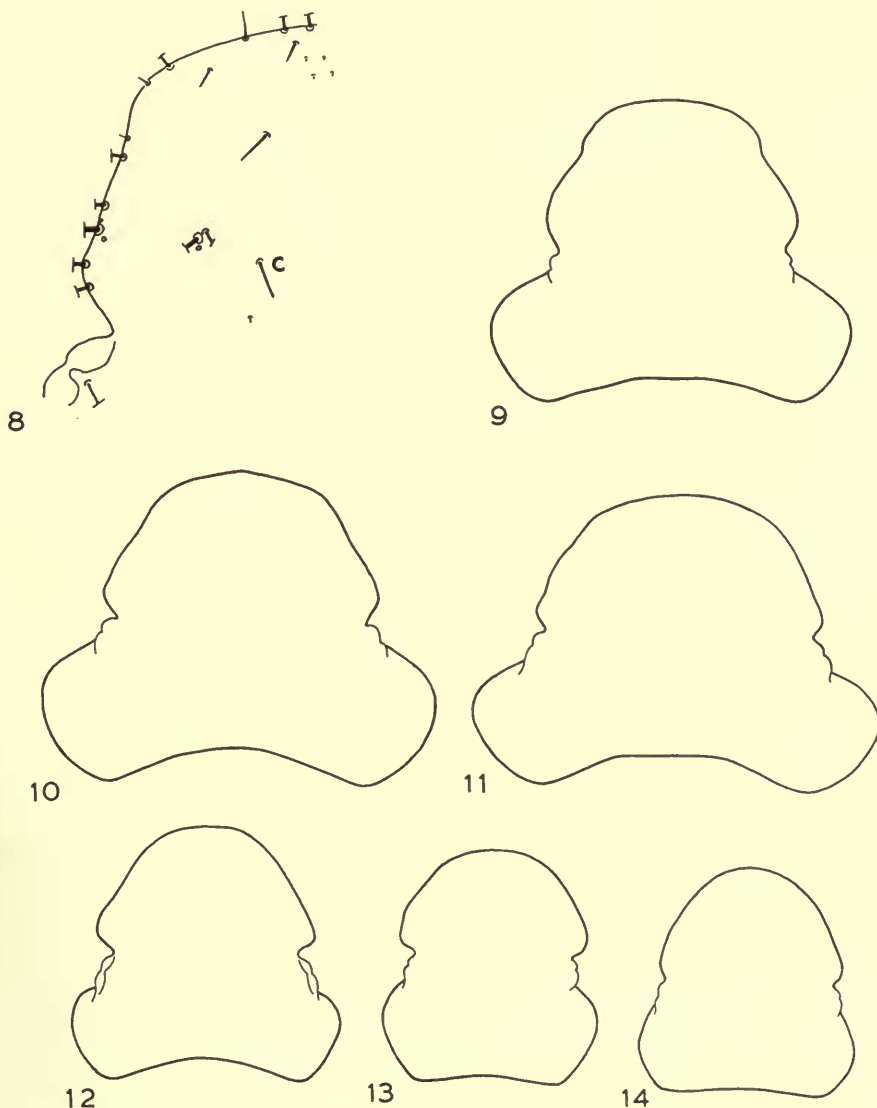
Included species (some of which are discussed in detail below) :

A. umbrinus, *A. pustulosus*, *A. totani*, *A. lyallpurensis*, *A. flumineus*, *A. paludosus*, *A. lacustris*, *A. limarius*, *A. spinulosus*, *A. limosae*, *A. kilauensis*, *A. multisetosus* and probably *A. stictus*.

There are three subdivisions of the *umbrinus* group.

Subdivision I

Specimens have been seen from species belonging to most of the genera of the subfamily Erolinae. These have the following characters: the prosternal plate does not surround the prosternal setae and is usually pointed posteriorly, but there is individual variation in this last character; there is also a tendency for individuals to have one long seta in the centre of the prosternal plate; the first dorsal pro-



FIGS. 8-14. Heads of *Actornithophilus* spp. 8. *A. incisus*, ♀. 9. *A. patellatus*, ♂. 10. *A. limosae*, ♀. 11. *A. ardeolae*, ♀. 12. *A. sabulosus* sp. n., ♂. 13. *A. erinaceus*, ♂. 14. *A. pediculoides*, ♂.

thoracic seta is relatively long and stout (Text-fig. 6), and the metanotum has long anterior setae. In the male, the tergites have a row of stout elongate submarginal setae and rows of smaller setae (Pl. 4, fig. 3), and the last tergite has anterior dorsal setae. The ventral thickening of the last segment of the female is in the form of two broad sclerites (Text-fig. 69). Sclerite of the genital sac as shown in Pl. VII, fig. 1.

The populations of the *umbrinus* group found on the Erolinae show a general correlation between average size of the individuals and the size of the host; correlated with increase in the size of the louse there is a tendency towards increase in the number of setae on some of the abdominal segments, but although the average number of setae is greater in the populations from the larger hosts, there is usually some overlap in numbers between the different populations. As the head becomes broader it tends to become proportionally shorter (Table I, Pl. 6, figs. 4-6) so that specimens from *Erolia subminuta* appear rather different from those from *Calidris canuta*; however, the populations from *Erolia minuta* and *E. testacea* show intermediates between those from the former two hosts so that subspecific division is unsatisfactory. *Ac.ornithophilus umbrinus* therefore will be used for the populations from *Erolia*, *Canuta*, *Crocethia*, *Ereunetes*, *Micropalama* and *Tryngites*. The synonymy of names included under *umbrinus sens. lat.* is given below.

The population from *Philomachus*, although resembling these populations, is distinguished by the less well developed lingual sclerites and epipharyngeal crest; by the female usually having no anterior setae on the last tergite (one individual amongst 26 examined had anterior setae); in the form of the sclerite of the genital sac (Pl. 10, fig. 2) and the shape of the last segment of the female abdomen. It is here recognized as a good species, *A. pustulosus*.

Actornithophilus umbrinus (Burmeister, 1838)

(Pl. 6, figs. 4-6, Pl. 7, fig. 3, Plate 10, fig. 1; Text-figs. 6, 19, 57, 69)

Colpocephalum umbrinum Burmeister, 1838. *Handb. Ent.* 2: 438. Host: *Tringa subarquata* = *Erolia testacea* (Pallas).

Colpocephalum umbrinum Burmeister. Giebel, 1874. *Insecta Epizoa*: 274, pl. 14, fig. 4.

Colpocephalum umbrinum Piaget, 1880. *Pediculines*: 556, pl. 46, fig. 6, nec *C. umbrinum* Burm. Host: *Tringa subarquata*.

Colpocephalum umbrosum, Harrison, 1916. *Parasitology*, 9: 56. *Nomen novum* for *C. umbrinum* Piaget nec Burmeister. **Syn. nov.**

Colpocephalum trilobatum Giebel, 1874. *Insecta Epizoa*: 275. Host: *Tringa minuta* = *Erolia minuta* (Leisler).

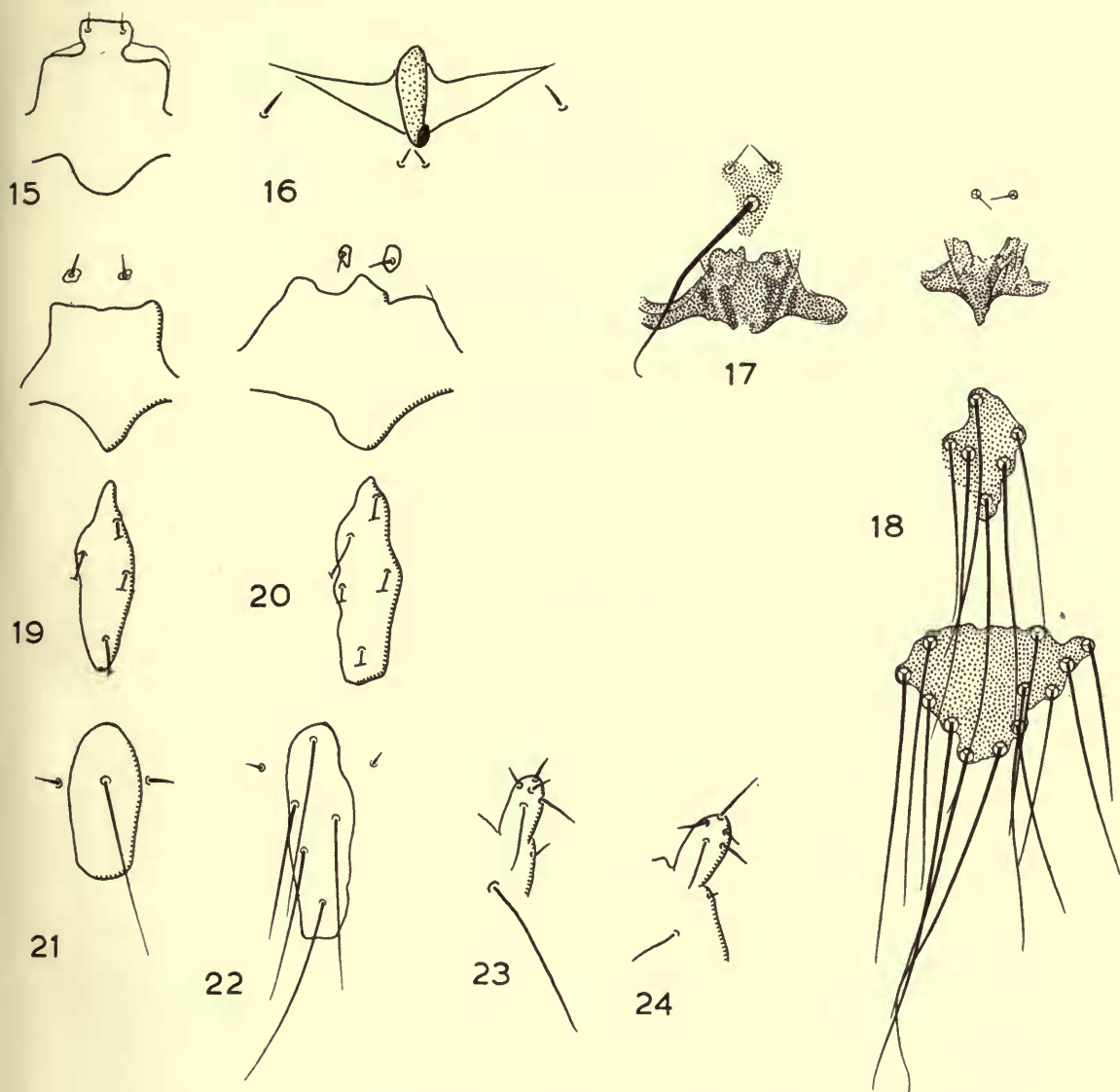
Colpocephalum morsitans Kellog & Mann, 1912. *Ent. News*, 23: 15, fig. 3. Host: *Tringa maculata* = *Erolia melanotos* (Vieillot).

Colpocephalum minor Kellogg & Chapman, 1899. *Occ. Pap. Calif. Acad. Sci.* 6: 112, pl. 7, fig. 9, nec *C. minor* Piaget, 1880. Host: *Calidris arenaria* = *Crocethia alba* (Pallas).

Actornithophilus albus Emerson, 1948. *Ent. News*, 59: 178, figs. 1, 2. Host: *Crocethia alba* (Pallas).

Actornithophilus hrabei Balát, 1953. *Folia zool. ent. Brno*. 2 (16): 8, fig. Host: *Calidris alpina* = *Erolia alpina* (Linn.).

Actornithophilus hirsutus Carriker, 1954. *Florida Ent.* 37: 139, fig. Host: *Ereunetes pusillus* (Linn.). **Syn. n.**



FIGS. 15-24. Fig. 15. *A. lyallpurensis*, male prosternal plate and setae. Fig. 16. *A. grandiceps*, anterior mesothoracic setae. Fig. 17. *A. pediculoides*, male prosternal plate and setae. Fig. 18. *A. sabulosus*, sp. n., male sternal plates of thorax. Figs. 19-20. Prosternal and mesosternal plates. 19. *A. umbrinus*. 20. *A. lacustris* sp. n. Figs. 21-22. Mesosternal plates. 21. *A. picus* from *Thalasseus bergii*. 22. *A. tetralicis* sp. n. Figs. 23-24. Labial palp. 23. *A. totani*. 24. *A. incisus* (Figs. 17-18. A. Smith del.).

Burmeister (1838) gave a short description of the specimen in the Nitzsch collection which was later figured in Giebel (1874). This figure appears to represent the *Actornithophilus* found on the type host. Piaget (1880) described and figured specimens from *Tringa subarquata* which he called *umbrinum*, but which he considered to be different from the figure in Giebel (1874); he suggested (557, 559) that the Nitzsch specimen had probably originated from *Philomachus pugnax*. However, the figure of a female in Giebel (1874) shows distinctly a number of setae on the dorsal surface of the last abdominal segment, which are not found in the population from *Philomachus pugnax* (one specimen from this host with one seta has been seen). There is one male in the Piaget collection labelled *Colpocephalum umbrinus* which is the species found on *Erolia testacea*. As already discussed above there seems no advantage in attempting to name the populations from the various species of *Erolia* and related genera and so the names which have been used are given above in the synonymy.

Neotype of *Colpocephalum umbrinum* Burmeister, 1838: ♂ in the British Museum (Natural History), slide No. 658 from *Erolia testacea* (Pallas) from North Cameroon collected by Dr. J. Mouchet, 1959.

Lectotype of *Colpocephalum umbrinum* Piaget: ♂ in the Piaget collection, British Museum (Natural History), slide No. 1379.

Measurements in mm.

A. umbrinus from *Erolia testacea*

	Male		Female	
	Length	Breadth	Length	Breadth
Head . . .	0.325	0.440	0.340	0.460
B.2 . . .	—	0.345	—	0.340
Prothorax . . .	—	0.330	—	0.340
Metathorax . . .	—	0.420	—	0.480
Abdomen . . .	1.040	0.505	1.290	0.630
Total . . .	1.720	—	2.010	—

Subdivision II

This subdivision comprises the populations from *Tringa* (including *Actitis*), and new species from *Catoptrophorus* and *Limnodromus*. *A. kilauensis* from *Heteroscelus* is probably also near this group but the only material seen from the type host is the lectotype female which is in poor condition. The classification of the populations from the different species of *Tringa* is difficult mainly due to the greater amount of individual variation in size and chaetotaxy than is usual in *Actornithophilus*. In most cases the number of specimens is small and it will be necessary to obtain larger series to make sure that the apparent differences in size between populations from the same host species from different localities (Tables III, VI) are not due to methods of collecting and preparation. Four groups (within the *totani* group) in addition to *A. paludosus*, well defined in the males at least, have here been recognized as species and are listed below with their hosts; the females cannot always be separated.

Host	<i>Actornithophilus</i> species from <i>Tringa</i> and <i>Actitis</i>		
<i>Tringa totanus</i> .	} <i>A. totani</i> (Schrank, 1803)	} <i>totani</i> group	
<i>Tringa erythropus</i>			
<i>Tringa flavipes</i> .			
<i>Tringa stagnatilis</i>			
<i>Tringa glareola</i> .	<i>A. totani</i> (Schrank, 1803) <i>sens. lat.</i>		
<i>Tringa ochropus</i> .	<i>A. lyallpurensis</i> Ansari, 1955		
<i>Actitis hypoleucos</i> .	<i>A. flumineus</i> sp. n.		
<i>Tringa nebularis</i> .	} <i>A. paludosus</i> sp. n.		
<i>Tringa melanoleuca</i>			

***Actornithophilus totani* (Schrank, 1803)**

Type host : *Tringa totanus* (Linn.)

(Pl. 11, fig. 1 ; Text-figs. 3, 23, 41, 59, 60)

Pediculus totani Schrank, 1803. *Fauna Boica* : 191. Host : " Strandschnepfen " = *Tringa totanus* (Linn.).

Colpocephalum affine Nitzsch, 1874. In Giebel, *Insecta Epizoa* : 276. Host : *Totanus maculatus* = *Tringa erythropus* (Pallas). **Syn. n.**

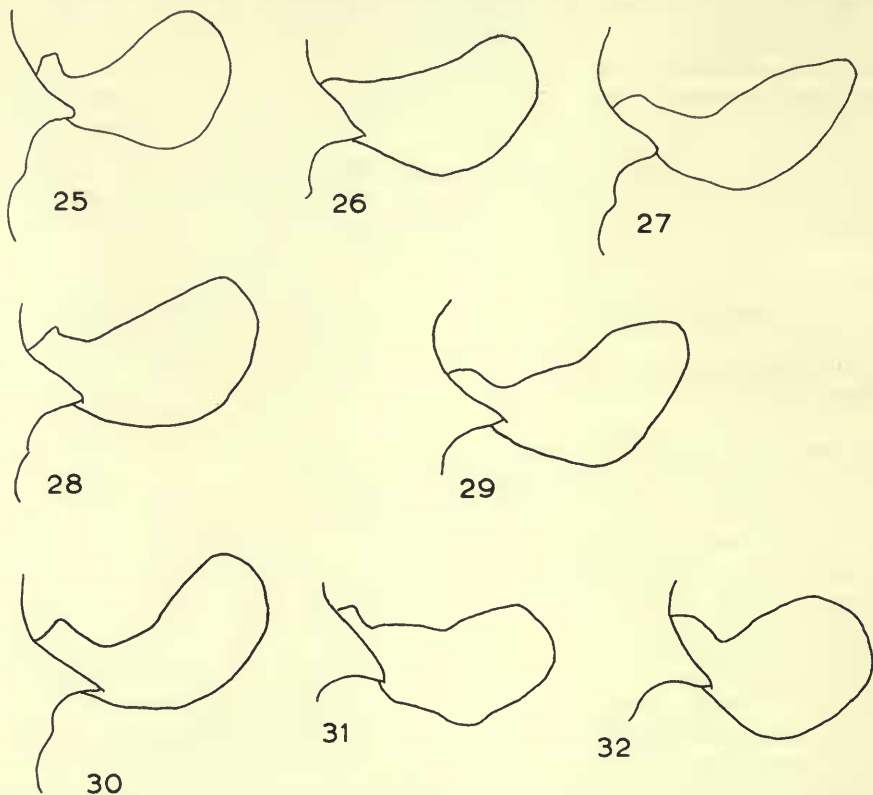
The history and interpretation of this name, the earliest to be used for an *Actornithophilus*, has been dealt with in Clay & Hopkins (1960 : 18).

MALE AND FEMALE. The species is distinguished from other forms belonging to this group by having no long anterior seta on the metanotum, by having anterior dorsal setae on the last segment of the abdomen in the male, by the size and arrangement of the male tergal setae (Text-fig. 3) and by the prosternal plate surrounding the prosternal setae. Genitalia as in Pl. 8, fig. 1 and Text-figs. 59–60. In the female at least two or more tergites have seven or more central setae and tergites II–VIII have a row of anterior setae. Genital region of female abdomen of the type shown in Text-fig. 71. Measurements in Tables III, IV and V.

The variation in the number of tergal setae of the male abdomen (Table II) means that individuals may appear considerably different from each other. Although the populations of which the average size of the individuals is smaller tend to have fewer setae this is not invariable, for instance one male from the same host individual as the neotype (Text-fig. 3) has the number of setae greatly reduced. In Table III the measurements of the breadth of the head at the temples of males is given for specimens from *Tringa totanus* from various localities. The numbers for some are small and in the females the differences are less and perhaps not significant. Fresher and more extensive material is required for a statistical analysis of these size relationships.

The populations from *Tringa totanus*, *T. erythropus*, *T. flavipes* and *T. stagnatilis* do not appear to be distinguishable from each other (Table IV). Specimens from *T. glareola* are difficult to place : the males have fewer tergal setae than is usual in *totani* but overlap with an occasional specimen from *Tringa totanus* which shows reduced tergal chaetotaxy ; one male said to have been taken from *T. glareola* in S. Africa has the tergal setae as in the new species from *A. hypoleuca* but differs in

the proportions of the head, suggesting that it may be an abnormal specimen of the population usually found on *Tringa glareola*. In the specimens available from *T. glareola* it is always possible to distinguish the females from *totani sens. str.* as all segments show marginal tergal pattern A, but further material may include an occasional specimen (as in *lyallpurensis*) with a greater number of tergoventral



FIGS. 25-32. Preocular nodi of *Actornithophilus* spp., males. Scale adjusted so that breadth at preocular enlargement is the same; actual breadth at temples in mm. of specimen given in brackets. Figs. 25-28. *A. ochraceus sens. lat.* 25. Host: *Charadrius tricollaris* (0.41). 26. Host: *Pluvialis apricaria* (0.48). 27. Host: *Chettusia gregaria* (0.51). 28. Host: *Squatarola squatarola* (0.49). Fig. 29. *A. gracilis* (0.51). Fig. 30. *A. uniseriatus* (0.55). Fig. 31. *A. himantopi* (0.49). Fig. 32. *A. mexicanus* (0.47).

setae. On the available material from *T. glareola* it would not be satisfactory to name the population, but as it shows some differences which indicate that it is perhaps rather distinct it is included in *totani* as *totani sens. lat.*

MATERIAL EXAMINED. 39 ♂, 43 ♀ from *Tringa totanus* (Linn.) from Iceland, British Isles, Estonia, Czechoslovakia, Morocco, Israel, Sudan, Ceylon; 4 ♂, 4 ♀ from *T. erythropus* (Pallas) from Yugoslavia, Czechoslovakia, India; 6 ♂, 5 ♀ from *Tringa stagnatilis* (Bechstein) from Sudan, East Africa and India; 10 ♂, 16 ♀ from *T. flavipes* (Gmelin) from various localities in N. America.

Neotype male (Text-fig. 3) and *neallotype* female of *Actornithophilus totani* (Schrank, 1803) in the Meinertzhagen collection, British Museum (Natural History) slide No. 11977a from *Tringa t. totanus* from Morocco, October, 1938.

***Actornithophilus flumineus* sp. n.**

Type host : *Actitis hypoleucos* (Linn.)

(Pl. 4, fig. 5)

This species is distinguished from *totani* by the shape of the head and by the smaller number of tergal setae, in which character it resembles *lyallpurensis*. It is distinguished from this latter species by the shape of the head and the presence of anterior dorsal setae on the last segment of the male.

MALE. As shown in Pl. 4, fig. 5. General characters of head, thorax, sternal chaetotaxy of the abdomen and male genital sclerite as in *totani*. Post-spiracular setae I, III and V shorter than II and IV but III not markedly shorter as in *totani*. Abdominal tergites I–VII with setal pattern A, VIII with 4, 5 or 6 central setae; tergites II–VIII usually with one row of anterior setae, but in some specimens some of the posterior tergites (V–VIII) may have two irregular rows; last abdominal segment with anterior dorsal setae.

FEMALE. Head and thorax as in male. Abdominal tergites I–VII with setal pattern A; VIII also usually with pattern A, one specimen has only three central setae. Tergites I–VIII may have a row of anterior setae, or I, VII and VIII may have only one or two anterior setae or VIII may have no anterior setae. Measurements of both sexes in Table V.

MATERIAL EXAMINED. 8 ♂, 12 ♀ from *Actitis hypoleucos* from various localities in Europe and Africa.

Holotype ♂ and *allotype* ♀ in the British Museum (Natural History), slide No. 7627 from the type host from Kenya, April, 1956. *Paratypes*: 7 ♂, 11 ♀ from the same host form with data as given above.

***Actornithophilus lyallpurensis* Ansari, ? 1955**

Type host : *Tringa ochropus* Linn.

(Text-fig. 15)

Actornithophilus lyallpurensis Ansari, ? 1955. *Proc. VIIth Pakistan Sci. Conf. (Agriculture)* : 55.

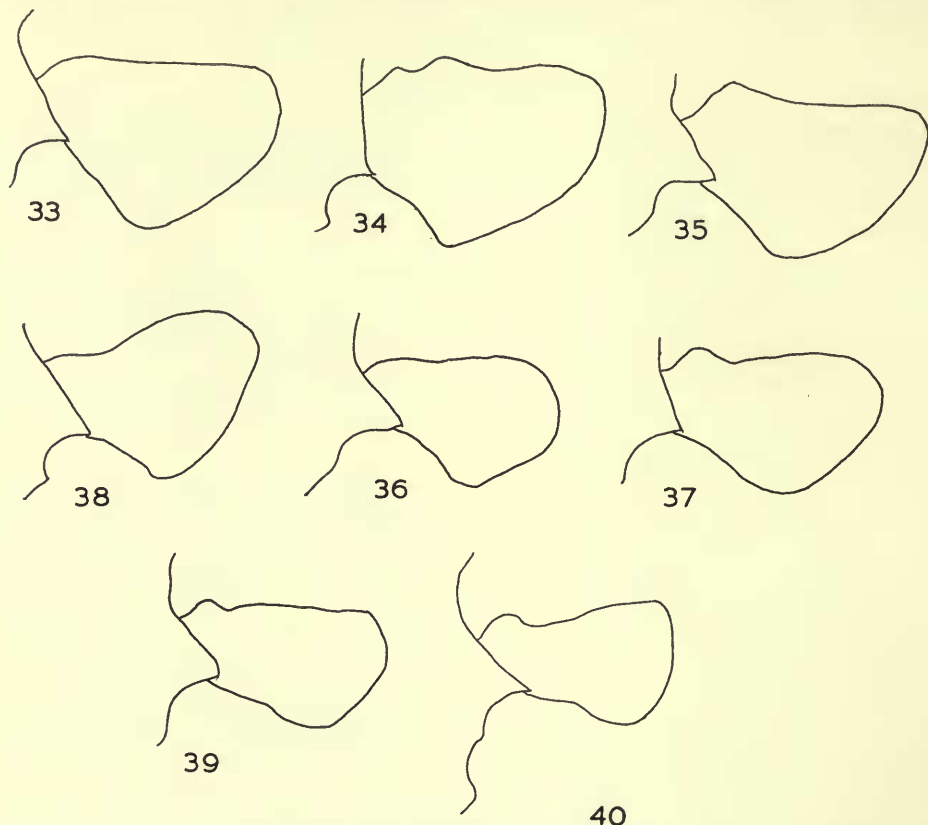
Type host : *Tringa ochropus* Linn.

Actornithophilus lyallpurensis Ansari, 1956. *Indian J. Ent.* **17** (1955) : 400.

Actornithophilus lyallpurensis Ansari, 1957. *Indian J. Ent.* **18** (1956) : 434, figs.

The species was described three times as a new species and it has not been possible to ascertain which is the earliest description as the date of publication of the first mentioned description is not known for certain. The measurements of the breadth of the head given in the original descriptions are different from those of specimens found on *Tringa ochropus* and given below (Table VII); however, it seems probable

that Ansari's description does refer to the population normally found on this host. This species is distinguished from *A. totani* by the abdominal chaetotaxy, and from *A. flumineus* sp. n. by the shape of the head and the absence of anterior dorsal setae on the last abdominal segment of the male. The small number of males seen show tergal pattern A on segments I, II and VII; on III, IV, V and VI the central



FIGS. 33-40. Preocular nodi of *Actornithophilus* spp., males. Scale as in Figs. 25-32. Figs. 33-37. *A. hoplopteri* sens. lat. 33. Host: *Hoplopterus spinosus* (0.49). 34. Host: *Lobibyx novaehollandiae* (0.51). 35. Host: *Chettusia leucura* (0.47). 36. Host: *Pluvianus aegyptius* (0.46). 37. Host: *Charadrius vociferus* (0.45). Fig. 38. *A. crinitus* sp. n. (0.51). Fig. 39. *A. pauliani* (0.51). Fig. 40. *A. tetralicis* sp. n. (0.58).

setae vary from six to eight; segment VIII usually has setal pattern A but may have only five central setae. Of the females seen all have setal pattern A on segments I-VII with the exception of two specimens with one and two segments respectively with seven central setae and one specimen which has the number of central tergal setae as follows: I, 6; II, 7; III, 10; IV, 7; V, 8; VI, 7; VII, 6. Tergite VIII has setal pattern A in all specimens seen with the exception of one specimen which has only four central setae. All the tergites may have a row of anterior setae, but on I and VIII the anterior setae may be reduced in number or absent.

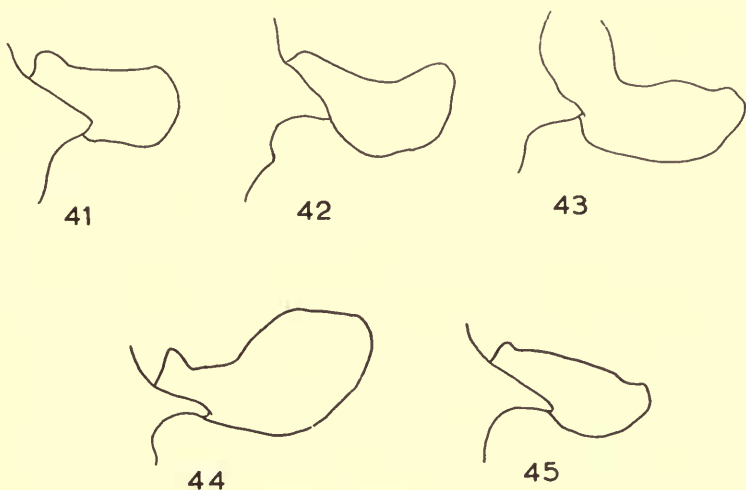
MATERIAL EXAMINED. 5 ♂, 10 ♀ from *Tringa ochropus* from Poland, Czechoslovakia and Israel.

***Actornithophilus paludosus* sp. n.**

Type host : *Tringa nebularia* (Gunnerus)

(Pl. 5, figs. 3, 6 ; Text-fig. 47)

This species is distinguished from the other species found on *Tringa* and *Actitis*. by the presence of long dorsal setae on the metathorax, by the prosternal plate not enclosing the prosternal setae and by the form of the sclerite of the genital sac.



FIGS. 41-45. Preocular nodi of *Actornithophilus* spp. Figs. 41-43 with scale as in Figs. 32-40 ; Figs. 44-45 to same scale. Fig. 41. *A. totani*, ♂. Fig. 42. *A. limosae*, ♀. Fig. 43. *A. ardeolae*, ♀. Fig. 44. *A. grandiceps*, ♀. Fig. 45. *A. spinulosus*, ♀.

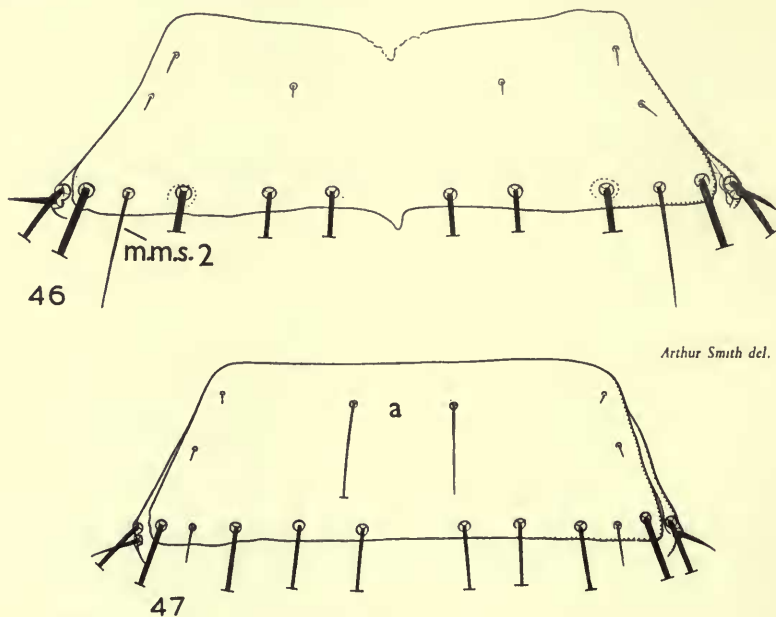
In many characters it resembles more closely the new species *A. lacustris* and *limarius* from *Catoptrophorus* and *Limnodromus*, although the general appearance of the tergal chaetotaxy is similar to that of *totani*.

MALE. As shown in Pl. 5, fig. 3. The prosternal plate does not surround the prosternal setae ; metathorax with two to four, occasionally one, long dorsal setae. Other characters of the head, thorax and abdomen as in *totani* with a similar range of variation of chaetotaxy. The small amount of material seen from *T. nebularia* falls into two size groups (see below), one from hosts collected in Aden and the Sudan and the other in Czechoslovakia ; those in the smaller size group tend to have fewer tergal setae, but there is some overlap in this character between the two groups. Last segment with anterior dorsal setae. The sclerite of the genital sac is longer and less triangular than in *totani* and more similar to that of *limosae*.

FEMALE. Head and thorax as in male, but two females from *T. melanoleuca* have no long dorsal setae on the metathorax. All tergites may have setal pattern

A, but the following range of tergo-central setae has been found: I, 6; II, 6-7; III, 6-11; IV, 6-10; V, 6-13; VI, 6-12; VII-VIII, 6. Two specimens from the same host have the following number of central setae: I, 6. 6; II, 6. 6; III, 6. 7; IV, 6. 10; V, 6. 13; VI, 6. 12; VII-VIII, 6. 6. The central tergites usually have two well-defined rows of setae but I, II, VII and VIII may have no anterior setae, one or two anterior setae or a well-defined row. Measurements of both sexes in Tables V, VI.

MATERIAL EXAMINED. 12 ♂, 19 ♀ from *Tringa nebularia* (Gunnerus) from Port Sudan, Aden, Burma and Czechoslovakia; 9 ♂ 13 ♀ from *Tringa melanoleuca* (Gmelin) from various localities in North America.



FIGS. 46-47. Metanotum of *Actornithophilus* spp. 46. *A. uniseriatus*. 47. *A. paludosus* sp. n. m.m.s. 2—marginal metathoracic seta 2; a.—long anterior setae of metanotum.

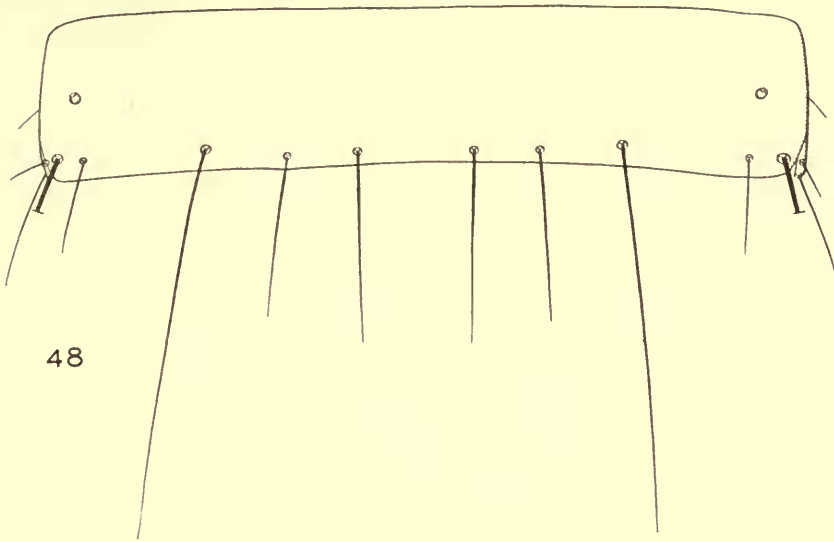
Holotype ♂ and *allotype* ♀ slide No. 16845 in the Meinertzhagen collection, British Museum (Natural History) from *Tringa nebularia* from Port Sudan, Sudan, December, 1947. *Paratypes*: 11 ♂, 18 ♀ from the same host form from localities given above.

Actornithophilus lacustris sp. n.

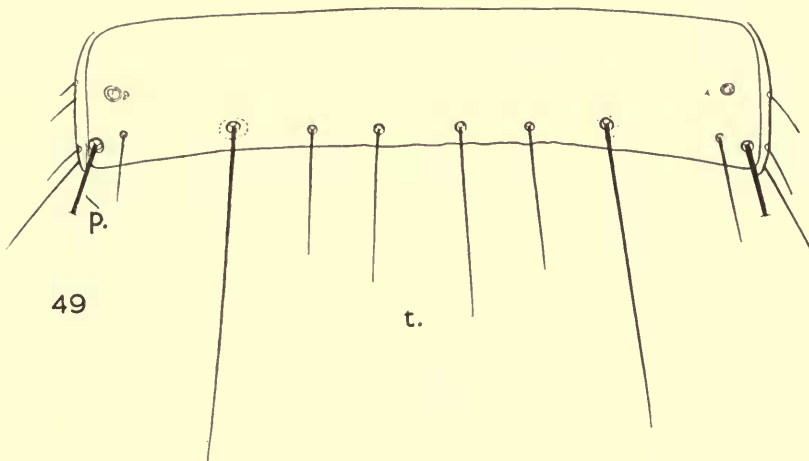
Type host: *Catoptrophorus semipalmatus inornatus* (Brewster)

(Pl. 5, figs. 1, 4, Pl. 11, fig. 5; Text fig. 20)

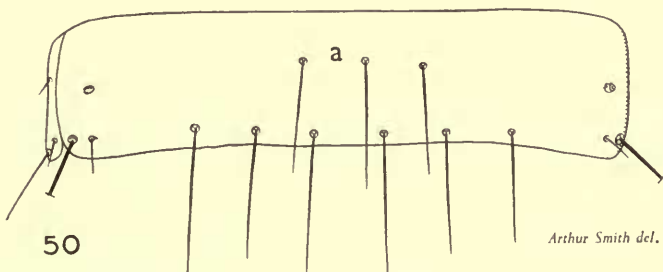
This species resembles most closely *A. limarius* and *A. paludosus* from which it can be separated by the size and number of tergal setae, size and shape of the head and by the prosternal plate usually having an anterior median projection.



48



49



50

Arthur Smith del.

FIGS. 48-50. Abdominal tergite V, male. 48. *A. tetralicis* sp. n. 49. *A. uniseriatus*. 50. *A. crinitus* sp. n. p.—post-spiracular seta; t.—6 tergocentral setae; a.—anterior tergal setae.

MALE. As shown in Pl. 5, fig. 1. Chaetotaxy of head and thorax as in *A. totani* except that dorsal head setae *d* are somewhat longer, the metanotum has long anterior setae, marginal prothoracic setae 5 and marginal metathoracic setae 2 tend to be longer and less fine and there are usually a greater number of setae on the meso- and metasternal plates. The prosternal plate does not surround the prosternal setae and usually has an anterior median projection (Text-fig. 20). Abdominal chaetotaxy similar to that of *totani* but differs in the density and size of the setae (Pl. 2, fig. 4); last segment with anterior dorsal setae. Genital sclerite as in Pl. 8, fig. 5.

FEMALE. Head and thorax as in male. Tergites I–VIII may have setal pattern A, but most specimens have two or more tergites with seven or more central setae; the allotype, for instance, has setal pattern A, while the tergo-central setae of another specimen are as follows: I, 6; II, 6; III, 7; IV, 7; V, 9; VI, 7; VII–VIII, 6; tergites I–VIII have anterior setae forming a definite row on most segments; last segment without anterior setae. Measurements of both sexes in Table VII.

The females of *A. lacustris* are not always easily distinguishable from those of *A. paludosus* unless both are available for comparison, especially when considering the relative length and thickness of the setae; these are stouter and longer in *A. lacustris*. In the latter host the females tend to be larger and most specimens have two or more tergites with seven or more central setae and the prosternal plate usually has an anterior median projection. In *A. paludosus* these characters may also occur and the measurements may overlap, but probably not all in the same specimen.

MATERIAL EXAMINED. 18 ♂, 19 ♀ from *Catoptrophorus semipalmatus inornatus* (Brewster) and *C. s. semipalmatus* (Gmelin) from California, Utah and Texas.

Holotype ♂ and *allotype* ♀ slide No. 12744a in the Meinertzhagen collection, British Museum (Natural History) from *Catoptrophorus semipalmatus inornatus* California, March, 1939. *Paratypes*: 17 ♂, 18 ♀ from the two forms of *C. semipalmatus*.

Actornithophilus limarius sp. n.

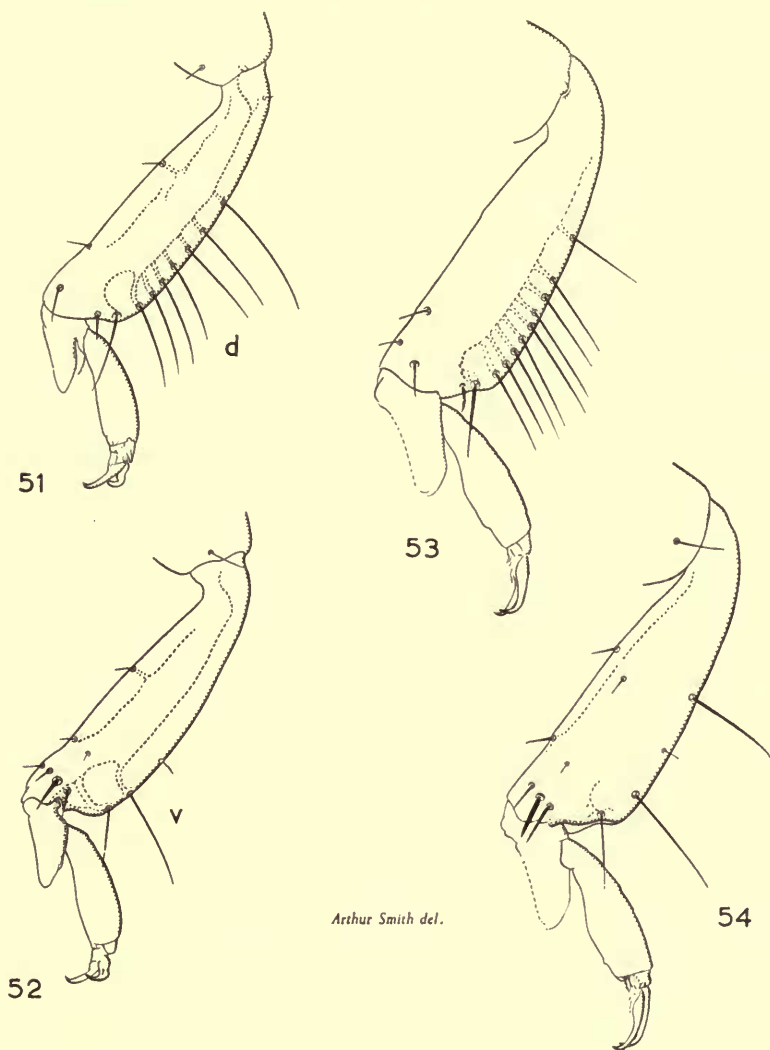
Type host: *Limnodromus griseus scolopaceus* (Say)

This species is separated from the two previous species by the size and number of tergal setae in both sexes.

MALE. As shown in Pl. 5, fig. 2. Except for size and shape, characters of head as in *A. lacustris* sp. n. Thorax and abdomen similar to that of *A. lacustris*, but the prosternal plate has no anterior median projection and is usually pointed posteriorly, although this last character may also occasionally be found in *A. lacustris*. Density and size of tergal setae as in Pl. 5, fig. 5. Last segment with anterior dorsal setae. Genital sclerite (Pl. 11, fig. 4) rather longer than in *lacustris*.

FEMALE. Head and thorax as in male. Tergal setae more numerous than in the last two species, the allotype, for instance, has the following number of tergo-central setae: I, 7; II, 10; III–V, 12; VI, 13; VII, 12; VIII, 6. Last segment with anterior dorsal setae. Measurements of both sexes in Table VII.

MATERIAL EXAMINED. 56 ♂, 45 ♀ from *Limnodromus griseus scolopaceus* (Say) from California and from *Limnodromus griseus* from South Carolina.



FIGS. 51-54. Third tibia. Figs. 51-52. *A. crinitus*. 51. Dorsal. 52. Ventral. Figs. 53-54. *A. tetralicis*. 53. Dorsal. 54. Ventral. d.—7 outer latero-dorsal setae; v.—3 outer latero-ventral setae.

Holotype ♂ and *allotype* ♀ slide No. 12734a in the Meinertzhagen collection, British Museum (Natural History), from *Limnodromus griseus scolopaceus*, California, March, 1939. *Paratypes*: 55 ♂, 44 ♀ from *Limnodromus griseus* with data as given above.

Actornithophilus kilauensis (Kellogg & Chapman, 1902)

Carriker (1957 : 103-104) in his notes on the Kellogg types in the Natural History Museum of Stanford University, mentions under this name a single female on slide 1210a which he considers automatically becomes the type of the species. Through the kindness of Dr. Paul Ehrlich, I have been able to see this slide. It is labelled "*Colp. n. sp. near timidum* (smaller). *Heteractitis incanus*. Hilo. 1901". It also has "1210a", "fig. ♀" and "desc" in pencil; it is labelled type. There is little doubt that it is one of the specimens referred to in the original description of *kilauensis* as the host and locality are correct and the species was said to resemble *timidum*. I have added a lectotype label to the slide with the specific name *kilauensis* (which otherwise does not appear) and the reference to Carriker, 1957. The specimen is in rather poor condition and has lost most of the setae, and although it is possible to see the number and position of these by their alveoli, nothing can be told of their length. According to the label, this was the figured specimen, but it does not in fact agree with pl. 14, fig. 1 (in Kellogg & Chapman, 1902) nor with the description, as the abdominal tergites of the specimen have a single line of marginal setae and not "numerous non-pustulated hairs scattered irregularly over the dorsal surface" and the last segment has no anterior dorsal setae. It is possible that the sternal setae have been shown on the dorsal surface or the description was made from a male which probably has anterior tergal setae. Unfortunately, no other specimens are available from the type host.

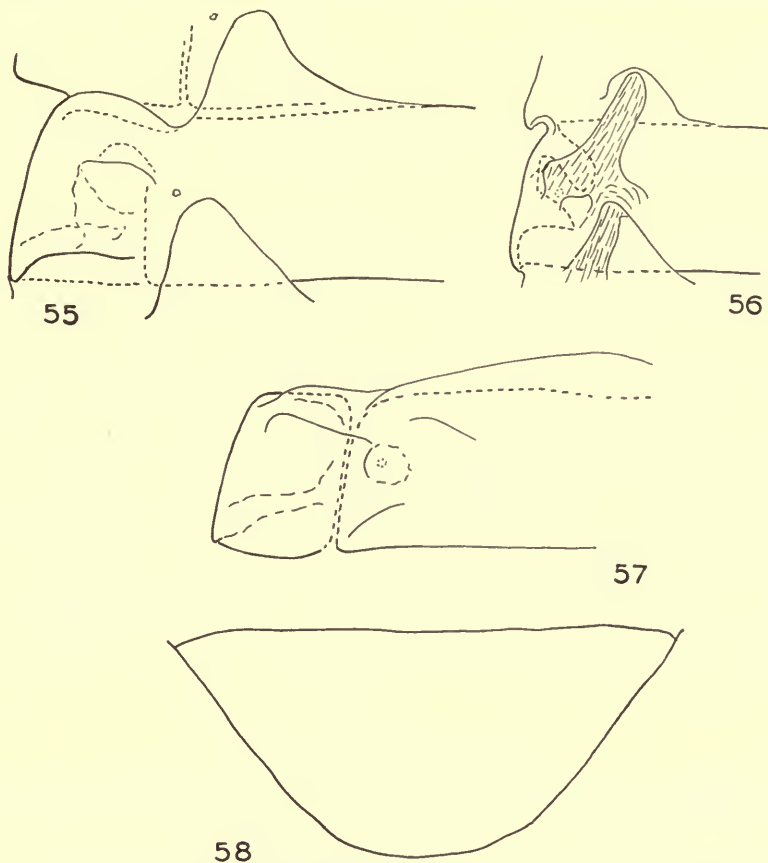
FEMALE. Shape of head as in Pl. 4, fig. 6. Dorsal prothoracic seta 1 small; all the marginal prothoracic setae are broken, but the alveoli of 5 are not as small as in those species where this seta is short and fine; prosternal plate partly hidden but probably surrounds setae, not strongly pointed posteriorly. Mesosternum: 5 setae; metasternum: 10; abdominal sternum I: 3 setae; II-III: 2 rows; IV-VII: 3 sparse rows. Brushes on IV with 23 and ? 22. Last sternites joined narrowly as in Text-fig. 71. The metanotum has no long anterior setae, marginal metathoracic seta 2 short but not fine. Tergites I-VIII with setal pattern A; III has 1 anterior seta; last segment without anterior dorsal setae. All the postspiracular setae are broken. Measurements in mm.: breadth of head at temples: 0.460; length of head: 0.340; breadth of prothorax: 0.315; metathorax: 0.400; breadth of abdomen: 0.565; length of abdomen: 1.080; total length: 1.765.

Subdivision III

The populations parasitic on the species of *Limosa* resemble each other within the *umbrinus* group by the following characters: the prosternal plate does not surround the prosternal setae; there are no long anterior setae on the metanotum, the tergites do not have well developed internal anterior processes; the males have anterior dorsal setae on the last segment and the tergal setae do not show pattern A.

Specimens have been seen from three species of *Limosa*: *L. limosa*, the type host of *A. spinulosus* (Piaget); *L. lapponica*, the type host of *A. limosae* (Kellogg) and *Limosa fedoa*. The males of *spinulosus* are at once distinguished from those of

limosae by the more numerous tergal setae but males from *Limosa fedoa* are intermediate between the two species in this character. Considering the males alone it might appear to be more convenient to include the populations from the three hosts under one name. The females, however, fall into two well-marked groups. Those of *limosae* and the population from *L. fedoa* have setal pattern A on seven to



FIGS. 55-58. Tergite IV to show internal anterior process. 55. *A. ochraceus*, segment opened out to show internal view. 56. *A. ochraceus*, as seen in whole mount. 57. *A. umbrinus*, internal view. 58. *A. tetralicis*, outline of last segment of ♀ abdomen.

five (rarely four) of the tergites and always on VII, whereas those of *spinulosus* have setal pattern A usually on only two (rarely three) tergites and never on VII. The females of *spinulosus* are also distinguished from those of *limosae* and the population on *L. fedoa* by the sternal thickening of the penultimate segment, which although showing individual variation in the exact outline, is separated into two sclerites (Text-figs. 67 and 68). The males of *spinulosus* can also be distinguished from the populations from the other two hosts by the size of the stout submarginal tergal setae relative to the rest of the tergal setae (Pl. 8, figs. 1-3). The following table

gives the mean head breadth of *Actornithophilus* specimens from the three species of *Limosa* and the crude mean of the wing lengths of the hosts arranged in order of the density of the tergal chaetotaxy, *A. limosae* having the smallest number of setae :

Parasite	Host	Mean head breadth of parasite (mm.)	Wing length (mm.)
<i>A. limosae</i>	<i>L. lapponica</i>	0.53 (9)	214
-----	<i>L. fedoa</i>	0.56 (16)	225
<i>A. spinulosus</i>	<i>L. limosa</i>	0.53 (5)*	221

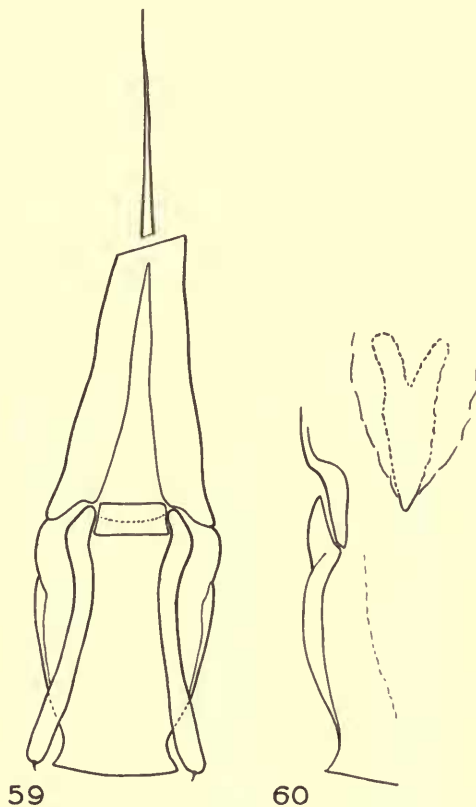
*This does not include the male lectotype, which although typical of the other specimens from *L. limosa* has a head breadth of 0.57 mm. The female paratype is also rather larger than the average; this may partly be due to overtreatment of the specimens with KOH.

Although the numbers, especially in the case of *spinulosus*, are small it appears that specimens from one of the larger hosts (*L. limosa*) do not average larger than those on the smallest host (*L. lapponica*), although they show an increase in the number of setae. Whereas in the case of specimens from the other larger host, *L. fedoa*, the specimens average larger than those from *A. lapponica* and also show an increase in the number of setae, this agrees with the rule usually found in related populations of *Actornithophilus*. The fact that specimens from *L. limosa* do not, on the evidence of present material, appear to follow this rule suggests that the population from this host may be less nearly related than are those on the other two hosts. Considering all these facts it is here decided to place the populations from *L. lapponica* and *L. fedoa* together under the name *limosae* in spite of differences in the density of the tergal setae in the male, and to recognize the population from *L. limosa* as a separate species, *A. spinulosus*. It is of interest that in *Austromenopon* the reverse is the case, the species parasitic on *L. fedoa* being the same as that on *L. limosa*, namely *A. limosae* Timmermann.

The *grandiceps* Group

This is a distinct group differing from all other known species from the Charadrii in that the majority of specimens do not have setal pattern A on the posterior dorsal margin of the metathorax (having a greater number of central setae), and by the females having two to three inner posterior setae each side of the last abdominal segment (Text-fig. 66). Timmermann (1954 : 836) is here followed in including the population from *Ibidorhynchus struthersii* under the name *A. grandiceps* (Piaget). Specimens (17 ♂, 18 ♀) collected from skins of this host from India, Tibet, Szechwan and N. Kansu have been seen. These are mostly in rather poor condition and it has not been possible to check the variation of certain characters in which they appear to differ from *A. grandiceps* from *Haematopus*. These are possibly the proportions of the head and last abdominal segment of the female, and the greater length of post-spiracular seta V relative to II in the females, but there are few specimens in which these setae are unbroken. The shape and size of the prosternal plate in specimens from both *Haematopus* and *Ibidorhynchus* vary considerably due to the degree of pigmentation of the plate. The mean of the number of tergocentral setae of the meta-

thorax is greater in specimens from *Ibidorhynchus*: in the 17 males examined only one specimen (in poor condition) probably had six central setae, the rest ranged from 9-15, with a mean of 10.59; a sample of 18 of *grandiceps* ranged from six (one specimen) to 11, with a mean of 8.72. The 18 females had a range of six (two



FIGS. 59-60. *A. totani*, male genitalia. 59. Ventral. 60. Dorsal.

specimens) to 16 tergocentral setae and a mean of 10.72; in 18 specimens of *grandiceps sens. str.*, one specimen had six setae, the range was 6-11 and the mean 8.47.

The *pediculoides* Group

This group contains two species: *A. pediculoides*, the systematic position of which has been discussed above (p. 191), and *A. sabulosus* sp. n. They resemble each other in the shallow preocular notch and reduction of the preocular nodi, in the small size of dorsal head setae *e*, the reduction of the prosternal plate, the rather sparse ventral chaetotaxy of the abdomen and the shape of the posterior margin of the mesosomal plate. The head is narrow at the temples in *pediculoides*, in which character it resembles *erinaceus*, and rather less so in *sabulosus*. It is difficult

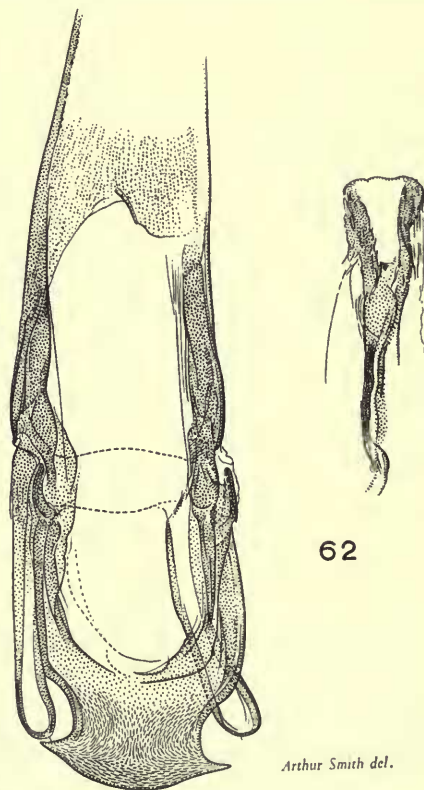
to say whether the two species are, in fact, related or only resemble each other due to some similarity of their habitats, perhaps both living in the quills as suggested above (p. 192).

Actornithophilus sabulosus sp. n.

Type host : *Charadrius hiaticula semipalmatus* Bonaparte

(Pl. 4, fig. 3, Pl. 9, fig. 1 ; Text-figs. 7, 12, 18, 61, 62)

This species is distinguished from *pediculoides* by the shape of the head, prosternal plate and the size of marginal prothoracic setae 1 and dorsal prothoracic setae 1.



61

62

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FIGS. 61-62. *A. sabulosus* sp. n. 61. Male genitalia, ventral. 62. Sclerite of genital sac.

MALE. General characters as shown in Pl. 4, fig. 3. Relative sizes of dorsal head setae e., dorsal prothoracic setae 1 and marginal prothoracic setae 1 and 5 as in Text-fig. 7. Metanotum without long anterior setae ; in the single male marginal metathoracic setae 2 vary in length and thickness on the two sides of the body. Tergites I-VIII with setal pattern A ; IV, V, VI and VII have one or two anterior setae, last segment without anterior dorsal setae. Sternal setae rather sparse,

sternites I–VII with two rows of setae in centre of segment; brush on IV as shown in Pl. 6, fig. 1. Ventral setae in the centre of the last segment eight in number and fewer than in the specimens of *pediculoides* examined, which have 10–14, but the number of setae here seems to be a variable character: two specimens of *A. ochraceus* from one host individual, for instance, have six and nine respectively. Genitalia as in Text-figs. 61–62.

FEMALE. Characters of head, thorax and chaetotaxy of tergites I–VIII as described for male except that there are seven mesosternal setae and nine metasternal. Sternites I–VII as described for male but there are three to four more setae in the brushes on segment IV. Last segment without anterior dorsal setae.

MATERIAL EXAMINED. 1 ♂, 1 ♀ from *Charadrius hiaticula semipalmatus* from Churchill, Manitoba, Canada, 17.vi.1934.

Holotype male and *allotype* female, slide No. 659 in the British Museum (Natural History) presented by Mr. G. H. E. Hopkins from *Charadrius hiaticula semipalmatus* Bonaparte with data as given above.

Measurements in mm.				
	Male		Female	
	Length	Breadth	Length	Breadth
Head (B.1)	0.355	0.410	0.380	0.410
(B.2)	—	0.330	—	0.330
Prothorax	—	0.330	—	0.325
Metathorax	—	0.430	—	0.440
Abdomen	1.460	0.580	1.540	0.600
Total	2.180	—	3.290	—

TABLE I.—*Breadths and Lengths of Male Head in mm. of A. umbrinus Populations from Various Hosts, with Ratio of Length of Head (L) to Breadth 1 and Crude Mean Wing Length in mm. of Male Hosts*

Host	Head of parasite							Wing length of male host (Crude mean)
	Breadth 1		Breadth 2		Length			
	Range	Mean	Range	Mean	Mean	$\frac{L}{B.1}$		
<i>Erolia subminuta</i> (2)	. 0.375-0.390	0.382	. 0.310	—	. —	—	. 94	
<i>E. minutilla</i> (20)	. 0.395-0.440	0.410	. 0.310-0.330	0.316	. 0.321	0.780	. 87	
<i>E. minuta</i> (5)	. 0.395-0.460	0.420	. 0.310-0.340	0.326	. 0.329	0.785	. 96	
<i>Ereunetes mauri</i> (8)	. 0.405-0.440	0.420	. 0.315-0.335	0.322	. —	—	. 94.6*	
<i>Erolia alpina</i> (22)	. 0.420-0.495	0.450	. 0.325-0.370	0.345	. 0.332	0.740	. 108	
<i>Erolia testacea</i> (7)	. 0.420-0.480	0.448	. 0.320-0.355	0.344	. 0.336	0.750	. 129	
<i>Erolia fuscicollis</i> (8)	. 0.415-0.475	0.451	. 0.330-0.360	0.350	. —	—	. 119.7*	
<i>Crocethia alba</i> (6)	. 0.450-0.480	0.460	. 0.340-0.370	0.350	. 0.337	0.730	. 123	
<i>Micropalama himantopus</i> (3)	. 0.450-0.475	0.465	. 0.345-0.360	0.365	. —	—	. 124.4*	
<i>Philomachus pugnax</i> (11)	. 0.490-0.540	0.520	. 0.370-0.400	0.386	. 0.350	0.675	. 192	
<i>Calidris canutus</i> (7)	. 0.510-0.550	0.530	. 0.390-0.420	0.405	. 0.367	0.690	. 166	

B.1, breadth at temples; B.2, breadth at preocular enlargement. Number of parasites measured in brackets.

*Average wing length as given in Ridgeway, 1919, *The Birds of North & Middle America*, vol. VIII.

TABLE II.—*Range of Tergal Setae of Male A. totani from Tringa totanus*

Anterior tergal setae†			Tergocentral setae† range
Segment	Range of 35 ♂		
I	1-5	.	4-7
II	3-7	.	6-12
III	3-11	.	8-22
IV	2-16	.	10-24
V	5-22	.	15-25
VI	9-20	.	15-25
VII	7-21	.	11-18
VIII	8-17	.	7-8
IX-XI*	2-12	.	—

†Numbers given in column under Anterior tergal setae are the number of setae (alveoli) in a square 0.11 × 0.11 mm. in the centre of the tergite omitting the marginal and large submarginal setae. The tergocentral setae are the small marginal and the larger slightly submarginal setae omitting the postspiracular and the seta next to it.

*Total number of dorsal anterior setae omitting the two long setae found on all species of *Actornithophilus*.

TABLE III.—*Mean and Range in mm. of Breadth of Head at Temples of Male A. totani from Tringa totanus from Various Localities*

Mean	Range	Number of specimens	Number of hosts	Locality	Host subspecies
0.513	0.480-0.550	11	2	Estonia	<i>t. totanus</i> .
0.502	0.455-0.530	6	4	Iceland, S. Uist	<i>t. robusta</i> .
0.497	0.490-0.505	2	1	E. Scotland	<i>t. subsp. ?</i>
0.488	0.480-0.495	3	1	Morocco	<i>t. totanus</i> .
0.468	0.455-0.480	3	3	British Isles	<i>t. totanus</i> .
0.457	0.450-0.465	2	2	Ireland	<i>t. subsp. ?</i>
0.456	0.445-0.465	6	4	India, Ceylon, Sudan	<i>t. eurhinus</i> .
0.455	0.450-0.460	2	2	British Isles	<i>t. britannica</i> .

TABLE IV.—*Measurements in mm. of Breadth of Head at Temples (1) and at Preocular Enlargement (2) of A. totani from Various Species of Tringa*

Male					
Host	Breadth 1		Breadth 2		
	Range	Mean	Range	Mean	
<i>Tringa totanus</i> *	0.45-0.53	0.49 (38)	0.33-0.38	0.36 (39)	
<i>T. erythropus</i> (4)	0.47-0.50	0.48	0.34-0.36	0.35	
<i>T. stagnatilis</i>	0.42-0.45	0.45 (6)	0.32-0.34	0.33 (4)	
<i>T. flavipes</i> (10)	0.41-0.47	0.45	0.31-0.35	0.33	
<i>T. glareola</i> (8)	0.40-0.48	0.44	0.29-0.36	0.32	
Female					
<i>Tringa totanus</i> (40)	0.48-0.57	0.52	0.35-0.41	0.38	
<i>T. erythropus</i> (4)	0.49-0.52	0.51	0.36-0.38	0.37	
<i>T. stagnatilis</i> (5)	0.46-0.49	0.47	0.35-0.36	0.35	
<i>T. flavipes</i> (10)	0.47-0.50	0.48	0.34-0.36	0.35	
<i>T. glareola</i> † (16)	0.43-0.50	0.45	0.32-0.36	0.33	

*See also Table III.

†Mean of breadth 1 of 10 specimens from the Sudan is 0.44 and of the remaining 6 from other localities is 0.47, the corresponding figures for breadth 2 are: 0.329 and 0.345; there are no males from the Sudan.

TABLE V.—Measurements in mm. of *Actornithophilus* Species

	Male									
	<i>totani</i>		<i>flumineus</i>		<i>paludosus</i>		<i>lacustris</i>		<i>limarius</i>	
	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth
Head	0.360	0.500	0.350	0.430	0.340	0.455	0.375	0.550	0.320	0.465
B.2	—	0.365	—	0.340	—	0.340	—	0.390	—	0.330
Prothorax	—	0.350	—	0.310	—	0.325	—	0.390	—	0.340
Metathorax	—	0.450	—	0.415	—	0.390	—	0.500	—	0.425
Abdomen	1.170	0.550	0.970	0.490	1.000	0.470	1.310	0.605	1.155	0.550
Total	1.930	—	1.700	—	1.680	—	2.120	—	1.850	—

Female

Head	0.370	0.520	0.370	0.470	0.350	0.490	0.380	0.535	0.350	0.490
B.2	—	0.385	—	0.360	—	0.360	—	0.380	—	0.350
Prothorax	—	0.365	—	0.330	—	0.335	—	0.370	—	0.350
Metathorax	—	0.510	—	0.480	—	0.435	—	0.500	—	0.480
Abdomen	1.490	0.700	1.300	0.640	1.420	0.610	1.450	0.730	1.380	0.665
Total	2.690	—	2.080	—	1.975	—	2.230	—	2.120	—

TABLE VI.—Measurements of Breadths of Head (in mm.) of *A. paludosus* from *Tringa nebularia* from Various Localities and from *T. melanoleuca*

Male

Host	Locality	Breadth 1		Breadth 2	
		Range	Mean	Range	Mean
<i>T. nebularia</i>	Port Sudan and Aden (4)	0.434–0.450	0.446	0.310–0.340	0.327
	Czechoslovakia (6)	0.500–0.520	0.504	0.355–0.360	0.360
<i>T. melanoleuca</i>	N. America	0.480–0.535	0.509	0.345–0.375	0.359

Female

<i>T. nebularia</i>	Port Sudan and Aden (8)	0.460–0.490	0.476	0.340–0.360	0.354
	Czechoslovakia (7)	0.500–0.550	0.517	0.360–0.380	0.368
<i>T. melanoleuca</i>	N. America	0.470–0.550	0.511	0.350–0.385	0.364

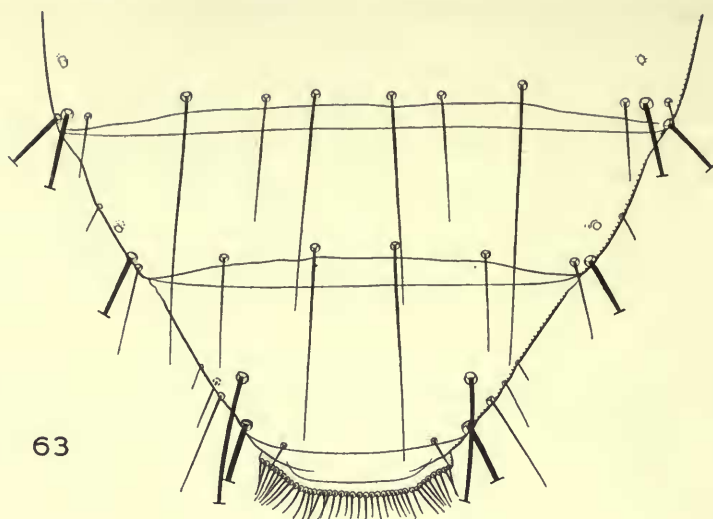
TABLE VII.—Measurements in mm. of Breadths of Heads of *Actornithophilus* sp.

Male

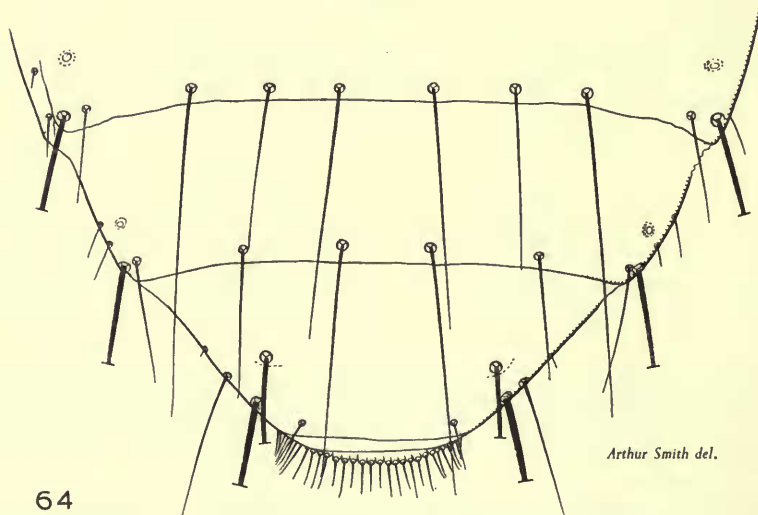
	Breadth 1		Breadth 2	
	Range	Mean	Range	Mean
<i>A. flumineus</i> (7)	0.40–0.45	0.43	0.31–0.34	0.33
<i>A. lyallpurensis</i> (5)	0.43–0.46	0.44	0.31–0.33	0.32
<i>A. lacustris</i> (10)	0.52–0.55	0.54	0.37–0.41	0.39
<i>A. limarius</i> (20)	0.46–0.48	0.47	0.33–0.35	0.34

Female

<i>A. flumineus</i> (11)	0.44–0.49	0.47	0.34–0.37	0.36
<i>A. lyallpurensis</i> (9)	0.45–0.49	0.47	0.33–0.35	0.34
<i>A. lacustris</i> (10)	0.53–0.56	0.55	0.38–0.41	0.39
<i>A. limarius</i> (20)	0.48–0.50	0.49	0.34–0.36	0.35



63



64

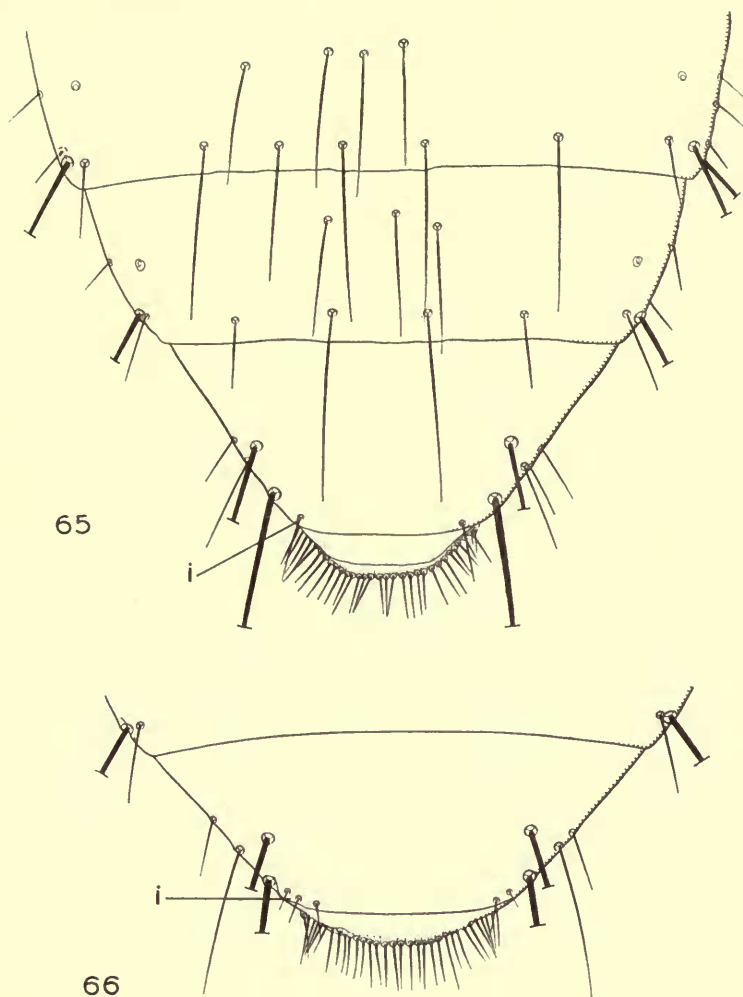
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FIGS. 63-64. Posterior tergites of female abdomen. 63. *A. ochraceus* from type host. 64. *A. sedes*.

NOTES ON THE INTERPRETATION OF CERTAIN NAMES

Actornithophilus perplanus (Kellogg & Chapman, 1899)

This species was based on a single specimen taken from one of the Alcae, *Lunda cirrhata*; the type specimen on slide 543b (see Carriker, 1957 : 104) has been seen and is a female belonging to the *ochraceus* group. Its size suggests that it originated from one of the larger Charadriinae (*sens.* Peters, 1934) such as *Squatarola squatarola* or *Pluvialis dominica*. A specimen of *Actornithophilus* from the former host is referred to in the same paper on p. 112. Thus the name *perplanus* would become



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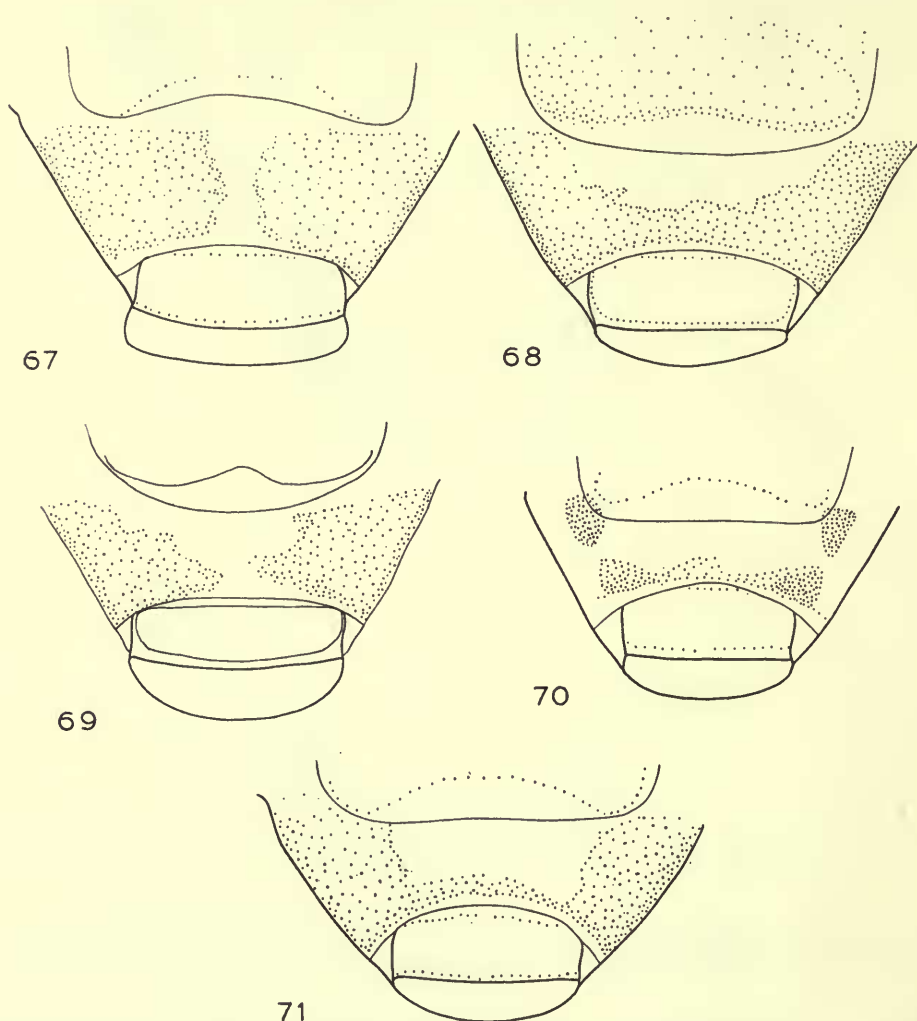
FIGS. 65-66. Posterior tergites of female abdomen. 65. *A. hoplopteri* from type host.
66. *A. grandiceps*. i.—inner posterior setae of last tergum.

a synonym of *flavipes* (Giebel, 1874), or *timidus* (Kellogg, 1896), if these were considered to be separable from *ochraceus* (Nitzsch, 1818), s. s., but as they have here been placed as synonyms of this latter name *perplanus* **syn. n.** becomes a synonym of *ochraceus*.

***Actornithophilus paetulus* (Kellogg & Kuwana, 1900)**

The description of this species was based on a single specimen, said to have been taken from *Arenaria interpres*, and which now cannot be found. It is difficult to

say what this specimen may have been, even whether it was a male or female, since it is referred to as a male in one place and a female in another. It has not been possible to find any *Actornithophilus* with long anterior setae on the metanotum and



FIGS. 67-71. Posterior sternites of female abdomen. 67. *A. spinulosus*. 68. *A. limosae*. 69. *A. umbrinus*. 70. *A. bicolor*. 71. *A. crinitus*.

with abdominal chaetotaxy as shown in the figure and with proportions of the head as given by the measurements. However, it may be an incorrectly figured specimen of the species normally found on *Arenaria*, that is *A. bicolor* (Piaget), but the name must remain a *nomen dubium* until the type specimen is found.

Colpocephalum subpustulatum Carriker, 1910

This species was based on a female from a kingfisher, *Ceryle alcyon*, and was almost certainly a straggler from one of the *Charadrii*. It is impossible to say what this specimen might have been as there is no *Actornithophilus* in which there is an

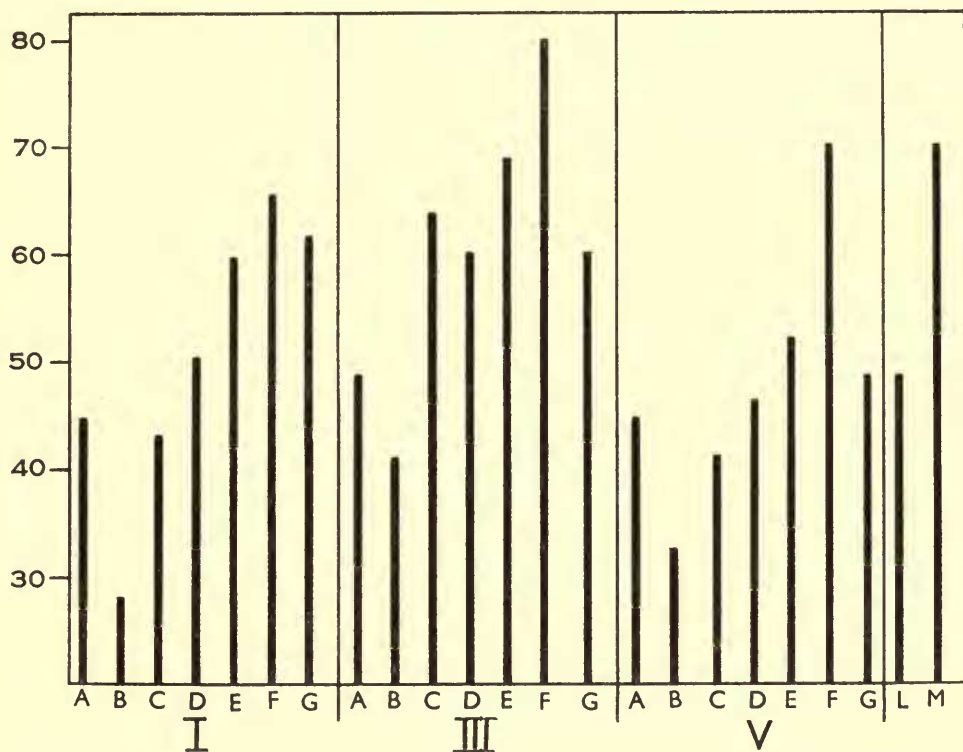


FIG. 72. Diagram showing relative lengths of post-spiracular setae I, III and V expressed as a percentage of II for individuals of species of *Actornithophilus*. A-G males of *Actornithophilus*: A. *ochraceus*; B. *hoplopteri*; C. *pauliani*; D. *himantopi*; E. *uniseriatus*; F. *tetracis*; G. *lacustris*. L-M. Post-spiracular seta III of females: L. *ardeolae*; M. *limosae*.

"absence of very long hairs on any portion of the body". It must therefore be presumed that the specimen was damaged and that the long setae were missing. If the "three irregular rows of fine short hairs" on the abdominal segments are dorsal, then the specimen might have belonged to the *umbrinus* species-group, if ventral possibly to the *ochraceus* group. However, without seeing the type specimen it is impossible to do more than guess about its identification.

Actornithophilus tigrus (Kellogg & Mann, 1912)

The original description was based on material from *Arenaria melanocephala* and *Aphriza virgata*. Carriker (1957 : 104) designated *Arenaria melanocephala* as the type host, but did not select a lectotype from the three specimens on slide 48b from this host to which he refers. This slide has been seen and although labelled as three males, the specimens are in fact females. In the original description reference is also made to three males, but there is little doubt that these females are the original material as the description of the colour, dorsal chaetotaxy and the four small blotches on segment " eight " of the abdomen fits the female of this species but not the male ; it was also stated that the genitalia were not visible. This slide has now been remounted and one of the females labelled as lectotype of *A. tigrus*. Specimens from *Arenaria melanocephala* do not appear to be separable from the population on *A. interpres*, so *tigrus* **syn. n.** becomes a synonym of *bicolor* (Piaget).

Actornithophilus scopularis (Neumann, 1912)

This was described from one male and two females taken from a *Passer domesticus* at Tring, England. The figure and description could apply to the *Actornithophilus* found on *Vanellus vanellus*, a likely bird to be found at Tring. However, the measurements given for the head do not seem to fit any species of *Actornithophilus* from the Charadrii either in actual measurements or in proportions ; the breadth of the head is similar to that of *grandiceps* from *Haematopus ostralegus* (not likely to be found at Tring), but the length is too great. Assuming that the measurements of the head are incorrect, it is possible that the specimens on which *scopularis* was based originated from *Vanellus vanellus* and were *A. gracile* (Paiget). However, unless the type is found this name must be considered a *nomen dubium*.

Actornithophilus raviensis Ansari, ? 1955

Actornithophilus raviensis Ansari, ? 1955. *Proc. VIIth Pakistan Sci. Conf. (Agriculture)* : 55.

Host : *Himantopus h. himantopus*.

Actornithophilus raviensis Ansari, 1956. *Indian J. Ent.* **17** (1955) : 400. Host : *Ibid*.

Actornithophilus raviensis Ansari, 1957. *Ibid.* **18** (1956) : 434, figs. Host : *Ibid*.

This species was described as new in all the publications given above and the first date of publication is uncertain. However, the description and figures make it probable that this name is a synonym of *himantopi* Blagoveshtchensky, 1951 from the same host, but this would have to be confirmed by an examination of the type. The measurements given in the description of the female holotype are too small for *himantopi* unless the specimen was in a shrunken condition ; the fact that the anterior margin of the head is distorted supports the last suggestion as this form of distortion has been seen in other shrunken specimens. The characters of the dorsal chaetotaxy and the figure of the prosternal plate fit those of *himantopi*.

KEY TO *ACTORNITHOPHILUS*¹

- 1 Seta at base of labial palp shorter than palp (Text-fig. 24); dorsal head sensillus 4 and dorsal head seta *d* absent (Text-fig. 8); mesosternal plate with one central seta² (Text-fig. 21); 1st outer latero-ventral seta of tibia III short and fine 2
- Seta at base of labial palp twice or more length of palp (Text-fig. 23); d.h. sensillus 4 and d.h. seta *d* present (Text-fig. 4); mesosternal plate with 3 or more central setae (Text-fig. 22); 1st outer latero-ventral seta of tibia III not short and fine (Text-fig. 52) 4
- 2 (1) Dorsal prothoracic setae 1 and 2 present; two inner posterior setae each side of last abdominal tergum; lateral preocular margins of head approximately perpendicular; ♂ with lateral head spines and asymmetrical genitalia 3
- D.p.s. 1 absent on at least one side; one inner posterior seta each side of last abdominal tergum (as in Text-fig. 65); head and genitalia not as above
- 3 (2) Abdominal tergites I–VIII without row of anterior setae *piceus sens. lat.* (p. 201)
- At least 3 abdominal tergites with row or rows of anterior setae *ceruleus* (p. 201)
- 4 (1) Metanotum with long anterior setae (Text-fig. 47) 5
- Metanotum without long anterior setae (Text-fig. 46) 14
- 5 (4) Abdominal pleurites without pattern of internal thickening; internal anterior processes undeveloped; tergites with never more than one row of anterior setae; tergum of last segment without anterior setae; shape of head characteristic (Text-fig. 9). (Prosternal plate with 1–2 elongated setae) *patellatus*
- Without above combination of characters 6
- 6 (5) D.p.s. 1 relatively long and stout (Text-fig. 6) 7
- D.p.s. 1 short and fine (Text-fig. 4) 9
- 7 (6) ♂ tergites with row of stout elongated submarginal setae and rows of smaller setae (Pl. 4, fig. 3); ♀ penultimate sternite broad and interrupted medially (Text-fig. 69) 8
- ♂ tergites with setae all of the same type (Pl. 4, fig. 4); ♀ penultimate sternite narrow and continuous across segment (as in Text-fig. 71). (Hypopharyngeal sclerites and epipharyngeal crest reduced; last tergum with anterior setae)
- 8 (7) Lingual sclerites and epipharyngeal crest reduced; male genital sclerite as in Pl. 7, fig. 2; tergum of last segment of ♀ usually without anterior setae *multisetosus*
- Lingual sclerites and epipharyngeal crest not reduced; male genital sclerite as in Pl. 7, fig. 1; tergum of last segment of ♀ with anterior setae *pustulosus*
- 9 (6) Males *umbrinus s. l.* 10
- Females 12
- 10 (9) Abdominal tergites I–VII with setal pattern A; head nodi large (Text-fig. 29); tergum of last segment without anterior setae. (Internal anterior processes of tergites well developed) *gracilis*
- Without above combination of characters 11
- 11 (10) Size and number of tergal setae as in Pl. 2, fig. 4; head b.1: 0.53–0.55, b.2: 0.38–0.41 mm.; male genital sclerite as in Pl. 8, fig. 5. Prosternal plate usually with anterior median projection (Text-fig. 20) *lacustris* sp. n. (Pl. 5, fig. 1)
- Size and number of tergal setae as in Pl. 2, fig. 6; head b.1: 0.43–0.52, b.2: 0.31–0.37 mm.; male genital sclerite long, similar to Pl. 8, fig. 4 *paludosus* sp. n. (Pl. 5, fig. 3)

¹All species recognized are included with the exception of *A. stictus*, *A. ocellatus* and *A. subpustulatus*, of which no specimens have been seen.

²Occasionally absent or two in number.

- Size and number of tergal setae as in Pl. 5, fig. 5; head b.1 : 0.46–0.48, b.2 : 0.33–0.35 mm.; male genital sclerite as in Pl. 11, fig. 4. (Prosternal plate without definite anterior median projection, tends to be pointed posteriorly) *limarius* sp. n. (Pl. 5, fig. 2)
- 12 (9) Tergite VII with setal pattern A; no anterior setae on last tergum 13
- Tergite VII with setal pattern otherwise; anterior setae on last tergum *limarius* sp. n.
- 13 (12) Head nodi large (Text-fig. 29); internal pleural thickening well developed and bilobed; prosternal plate surrounds setae; tergite VIII with sternal pattern A.1 *gracilis*
- Without above combination of characters *lacustris, paludosus* (p. 222)
- 14 (4) D.h.s. ϵ small (Text-fig. 7); pleurites without well-marked pattern of internal thickening; tergites I–VII with setal pattern A; posterior margin of mesosome with well-marked pointed projections each side (Text-fig. 59) 15
- Without above combination of characters 16
- 15 (14) Preocular emargination (Text-fig. 12) and prosternal plate (Text-fig. 18) characteristic; m.p.s. 1 and d.p.s. 1 long (Text-fig. 7) *sabulosus* sp. n. (Pl. 4, fig. 3)
- Preocular emargination (Text-fig. 14) and prosternal plate (Text-fig. 17) characteristic; m.p.s. 1 and d.p.s. 1 shorter (similar to Text-fig. 6) *pediculoides*
- 16 (14) Males 17
- Females 34
- 17 (16) Tergum of last abdominal segment without anterior setae 18
- Tergum of last abdominal segment with anterior setae 29
- 18 (17) Tergites VI and VII at least with tergal pattern A 19
- Tergites VI and VII with more central setae 28
- 19 (18) Preocular and occipital nodi small (as in Text-fig. 41); d.p.s. 1 minute (Text-fig. 4); sclerite in sac as in *A. totani* (Text-fig. 60). (Tergal setae each side of p.sp.s. of VIII long, central setae of tergite VIII long and stout; tergites II–VIII each with a well-marked row of anterior setae; leg setae sparse) *lyallpurensis*
- Without above combination of characters 20
- 20 (19) Setae of brush on 3rd femora and sternite IV (Pl. 9, fig. 5) numerous; latero-ventral setae of tibiae II–III: 3 long and 1–2 short and fine (Text-fig. 53); outer latero-dorsal tibial setae of III 7–9 (Text-fig. 54). Post-spiracular setae III and V not markedly shorter than II and IV (Text-fig. 72); male genital sclerite as in Pl. 10, fig. 6 *tetracis* sp. n. (Pl. 4, fig. 2)
- Without above combination of characters 21
- 21 (20) Sclerite of genital sac as in Pl. 10, fig. 5. (Nodi well developed, Text-figs. 33–37, tergites I–VII with setal pattern A, VIII with A.1) 22
- Sclerite of genital sac otherwise (Pl. 10, figs. 3, 4) 23
- 22 (21) Prosternal setae not surrounded by prosternal plate; post-spiracular setae I and III (Text-fig. 72) and tergal setae longer than in *hoplopteri* (Pl. 7, fig. 2) *pauliani*
- Prosternal setae surrounded by prosternal plate; post-spiracular setae I and III (Text-fig. 72) and tergal setae shorter (Pl. 7, fig. 1) *hoplopteri* s. l.
- 23 (21) Preocular enlargement with 3–4 setae on both sides of head (Text-fig. 4). Two or more tergites with row of anterior setae; tergal setae rather short and stout; sclerite of genital sac as in Pl. 10, fig. 4. *crinitus* sp. n. (Pl. 4, fig. 1)
- Without above combination of characters 24
- 24 (23) M.p.s. 5 (Text-fig. 5) and m.m.s. 2 (Text-fig. 46) usually not short and fine; d.p.s. 1 not minute (cf. Text-figs. 5 and 4); inner tergo-central setae of II–VI markedly shorter than the outer setae (Text-fig. 49); p.sp.s. III relatively longer than that of *ochraceus* and *hoplopteri* (Text-fig. 72) 25
- Without above combination of characters 27

- 25 (24) D.h.s. *a* spine-like ; head as in Pl. 6, fig. 2 *mexicanus*
 — D.h.s. *a* not spine-like 26
- 26 (25) At least one tergite normally with 7 or more central setae. Head as in
 Pl. 6, fig. 1 *uniseriatus*
 — All tergites normally with 6 central setae. Head as in Pl. 6, fig. 3 *himantopi*
- 27 (24) Sides of abdomen rounded and shape of head as in Pl. 4, fig. 4 ; sclerite of
 genital sac as in Pl. 11, fig. 2 *sedes*
 — Sides of abdomen more parallel and shape of head as in Text-fig. 2 ; genital
 sac as in Pl. 10, fig. 3 *ochraceus sens. lat.*
- 28 (18) Tergite I with one marginal row of setae and sometimes 1-2 anterior setae ;
 metanotum with marginal setal pattern A ; head as in Pl. 7, fig. 5 *ardeolae*
 — Tergite I with one marginal and one anterior row of setae ; metanotum with
 marginal pattern usually otherwise *grandiceps*
- 29 (17) Tergites I-VII with tergal pattern A ; head as in Pl. 4, fig. 5 *flumineus* sp. n.
 — Tergites I-VII with setal pattern otherwise 30
- 30 (29) Pleurites narrow ; shape of head as in Text-fig. 13 *erinaceus*
 — Not as above 31
- 31 (30) Tergites II-VIII with 2 submarginal setae each side (excluding the p.sp.s.)
 considerably longer and stouter than marginal row (Pl. 9, fig. 6) ; prosternal
 setae not surrounded by prosternal plate ; sclerite of genital sac distinctive
 (Pl. 11, fig. 3) *bicolor*
 — Without above combination of characters 32
- 32 (31) Prosternal setae surrounded by prosternal plate ; genital sclerite short (Text-
 fig. 60) ; usually not more than 4-5 mesosternal setae *totani* (Text-fig. 3)
 — Without above combination of characters 33
- 33 (32) Stout submarginal setae of tergite VIII thicker relative to rest of dorsal setae,
 number of fine marginal setae greater (Pl. 8, fig. 3) than in *limosae* *spinulosus*
 — Stout submarginal setae of tergite VIII less thick relative to rest of dorsal
 setae, number of finer marginal setae less (Pl. 8, figs. 1 and 2) *limosae* s. l.
- 34 (16) Temples scarcely expanded (as in ♂, Text-fig. 13) ; pleurites with stout spines.
 (Tergites I-VIII with setal pattern A and one anterior row of setae) *erinaceus*
 — Without above combination of characters 35
- 35 (34) Prosternal setae not surrounded by prosternal plate ; sclerites of genital region
 characteristic (Text-fig. 70) ; m.m.s. 2 stout ; tergites I-VIII with setal
 pattern A, VIII occasionally has A.1, no rows of anterior setae *bicolor*
 — Without above combination of characters 36
- 36 (35) Tergite VII with 8 or less central setae 38
 — Tergite VII with 10 or more central setae. (At least 5 tergites with anterior
 setae) 37
- 37 (36) Head nodi small (Text-fig. 45) ; metanotum with marginal setal pattern A ;
 last tergum with one inner posterior seta *spinulosus*
 — Head nodi larger (Text-fig. 44) ; metanotum with marginal setal pattern usually
 otherwise ; last tergum with 2-3 inner posterior setae (Text-fig. 66) *grandiceps*
- 38 (36) Head nodi of medium size (Text-fig. 43) ; d.p.s. 1 rather stout ; m.p.s. 5 elongate,
 m.m.s. 2 stout ; at least 3 tergites with more central setae than in pattern A,
 at least 4 tergites with an anterior row of setae ; shape of head as in Text-fig.
 11 *ardeolae*
 — Without above combination of characters 39
- 39 (38) Mesosternum with 7-11 setae ; prosternal setae not surrounded by prosternal
 plate ; head nodi small (Text-fig. 42) ; shape of head as in Text-fig. 10. At
 least 3 tergites with a row of anterior setae *limosae* s. l.
 — Without above combination of characters 40
- 40 (39) Head nodi small (Text-fig. 41) 41
 — Head nodi not small (Text-figs. 25-40) 43

- 41 (40) Tergites without anterior setae *kilauensis*
 — Tergites with anterior setae on at least 3 segments 42
- 42 (41) Prosternal setae not surrounded by prosternal plate . . . *paludosus* sp. n. (p. 222)
 — Prosternal setae surrounded by prosternal plate (Text-fig. 15) *totani* group (p. 215)
- 43 (40) Preocular enlargement with 3-4 setae on both sides of the head (Text-fig. 4);
 (Tergites I-VII with setal pattern A, VIII with setal pattern A.1; anterior
 setae on some tergites) *crinitus* sp. n.
 — Without above combination of characters 44
- 44 (43) Setae of brush on 3rd femora and sternite IV (Pl. 9, fig. 5) and outer lateral
 margins of tibiae more numerous than in the following species; outer latero-
 ventral setae of tibiae II-III: 3 long and 1-2 short and fine, outer latero-
 dorsal setae: 7-10 (Text figs. 53-54). P.sp.s. III and V not markedly
 shorter than II. Shape of head as in male (Pl. 4, fig. 2) . . . *tetralicis* sp. n.
 — Without above combination of characters 45
- 45 (44) Tergites I-II, VI-VII at least, usually with setal pattern A, total central setae
 on tergites II-VII less than 44, known range 36-39 47
 — Tergites II-VI at least with more central setae, total central setae of tergites
 II-VII more than 44, known range 48-54 46
- 46 (45) Breadth of head, known range: 0.57-0.61 mm. *uniseriatus*
 — Breadth of head, known range 0.50-0.51 mm. *mexicanus*
- 47 (45) D.p.s. 1 rather stout (as in Text-fig. 5); p.m.s. 5 elongated; m.m.s. 2 rather
 stout; head shape as in ♂ (Pl. 6, fig. 3) *himantopi*
 — Without above combination of characters 48
- 48 (47) Prosternal setae not surrounded by prosternal plate. (At least 3 tergites with
 row of anterior setae) *pauliani*
 — Prosternal setae surrounded by plate 49
- 49 (48) Outer tergocentral setae of VII reach nearly or to end of abdomen, shape of
 last segment as in Text-fig. 64; sides of abdomen rounded . . . *sedes*
 — Outer tergocentral setae of VII shorter, shape of last segment as in Text-figs.
 63, 65; sides of abdomen more parallel 50
- 50 (49) Anterior edge of preocular nodus usually straighter (Text-figs. 33-37); outer
 tergocentral setae of VIII short (Text-fig. 65) *hoplopteri* s. l.
 — Anterior edge of preocular nodus usually indented (Text-figs. 25-28); outer
 tergocentral seta of VIII longer (Text-fig. 63) *ochraceus* s. l.

GLOSSARY

Anterior tergal setae. The setae anterior to the row along the posterior margin of the tergite (Text-fig. 50, a); in the key the term is used for the setae in the centre of the segment as laterally there may be extra setae when centrally there is only one row. The anterior setae of the last tergum are the shorter setae anterior to and level with the long lateral setae always found on the dorsal surface of the last abdominal segment in both sexes. The long anterior setae of the metanotum are the longer setae found in the central area of the metanotum in some species (Text-fig. 47, a).

Breadth of the head; b.1 and b.2. B.1 = breadth at temples, b.2 = breadth at preocular enlargement.

Dorsal head sensilli (d. h. sens.) 1-4. These have been discussed elsewhere (Clay, 1961) and are shown here in Text-fig. 4.

Dorsal head setae (d. h. s.) a-f. These setae may show useful taxonomic characters (Text-fig. 4).

Dorsal prothoracic seta (d. p. s.) 1-2. See Text-fig. 4.

Inner posterior setae of last tergum. In most of the species of *Actornithophilus* there is one short seta each side of the posterior margin of the last tergum of the female (Text-fig. 65); in *A. grandiceps* (Text-fig. 66) there are two to three each side, although the occasional specimen may have only one.

Internal anterior process of tergite. The size of this varies considerably in different species (Text-figs. 55-57 and Pl. 7, fig. 1).

Male genital sclerite. The sclerite in the genital sac of the male genitalia, the form of which may be of taxonomic value (Pls. 10 and 11).

Marginal prothoracic seta 5 (m. p. s. 5). Although this seta tends to show individual variation in length and thickness, in some species it is normally short and fine and in others longer and stouter (Text-figs 4 and 5). This also applies to m.m.s. 2 see below.

Marginal metathoracic seta 2 (m. m. s. 2). See above under m.p.s. 5 and Text-figs. 46 and 47.

Marginal tergal setae of metathorax and abdomen. In many species of *Actornithophilus* the marginal setae of the tergites are arranged from the lateral margin inwards as follows: the long stout post-spiracular seta followed by a shorter seta; between these two setae, which lie each end of the tergite, is a row of six setae (the tergo-central setae); this arrangement is referred to as Setal Pattern A (Text-fig. 49). In some groups of species tergite VIII has only four central setae and this is referred to as A.1 (Text-figs. 63 and 64). The occasional specimen may have one or two segments in which there is an extra seta. In some species where the central tergal setae are more numerous there may be six stouter and longer, sometimes submarginal, setae which may represent the usual six central setae of pattern A. In certain groups of species (*i.e. ochraceus* and *hoplopteri*) this pattern is quite constant, in other species there may be some specimens which show setal pattern A on certain segments and others in which these segments have a greater number of central setae. In the majority of species from the Charadriidae the metanotum also has setal pattern A, but in *A. grandiceps* there are usually more central setae.

Post-spiracular setae (p.sp.s). See Text-fig. 49.

Preocular enlargement. The enlargement of the lateral margin of the head anterior to the preocular notch.

Preocular nodus. The patch of thickening surrounding the preocular notch (Text-figs. 33-45).

Prosternal setae. The two small setae in the centre of the prosternum which may (Text-fig. 15) or may not (Text-fig. 19) be surrounded by the prosternal plate. There may also be a long central seta posterior to these (Text-fig. 17).

Setal pattern A and A.1. See under marginal setae.

LIST OF SPECIES OF *ACTORNITHOPHILUS* PARASITIC
ON THE CHARADRIIFORMES

Names considered to be synonyms in Hopkins & Clay (1952), are not repeated here.

* Denotes that the holotypes or paratypes have been seen ; † that specimens have been seen from the type host.

Species	Type host	Comments
† <i>affinis</i> (Nitzsch), 1874	<i>Tringa erythropus</i>	= <i>totani</i> (Schrank).
† <i>albus</i> Emerson, 1948	<i>Crocethia alba</i>	= <i>umbrinus</i> (Burmeister) s. l.
* <i>ardeolae</i> Timmermann, 1954	<i>Dromas ardeola</i>	
† <i>bicolor</i> (Piaget), 1880	<i>Arenaria i. interpres</i>	
<i>brachycephalus</i> (Giebel), 1874	<i>Stercorarius pomarinus</i>	Probably straggler ; unidentifiable.
† <i>candidus</i> Carriker, 1949	<i>Gygis alba candida</i>	p. 201.
* <i>ceruleus</i> (Timmermann, 1954)	? <i>Procelsterna c. cerulea</i>	Correct host doubtful (p. 201)
* <i>crassipes</i> (Piaget, 1880)	<i>Thalasseus bergii cristatus</i>	= <i>piceus</i> (Denny).
* <i>crinitus</i> sp. n.	<i>Stephanibyx c. coronatus</i>	p. 205.
† <i>epiphanes</i> (Kellogg & Chapman, 1902)	<i>Anous stolidus pileatus</i>	= <i>incisus</i> (Piaget).
* <i>erinaceus</i> Timmermann, 1954	<i>Rostratula benghalensis</i>	
† <i>flavipes</i> (Giebel, 1874)	<i>Squatarola squatarola</i>	= <i>ochraceus</i> (Nitsch) s. l.
* <i>flumineus</i> sp. n.	<i>Actitis hypoleucos</i>	p. 217.
<i>funnebris</i> (Kellogg, 1896)	<i>Larus glaucescens</i>	= <i>piceus</i> (Denny) s. l.
* <i>fuscipes</i> (Piaget, 1880)	<i>Larus dominicanus</i>	= <i>piceus</i> (Denny) s. l.
* <i>gracilis</i> (Piaget, 1880)	" <i>Platalea alba</i> " Error	True host probably <i>Vanellus vanellus</i> (p. 202).
* <i>grandiceps</i> (Piaget, 1880)	<i>Haematopus ostralegus</i>	p. 226.
† <i>himantopi</i> (Blagoveshtchensky, 1951)	<i>Himantopus h. himantopus</i>	p. 208.
† <i>hirsutus</i> Carriker, 1954	<i>Ereunetes pusillus</i>	= <i>umbrinus</i> (Burm.) s. l.
† <i>hoplopteri</i> (Mjöberg, 1910)	<i>Hoplopterus spinosus</i>	p. 202.
* <i>hrabei</i> Balát, 1953	<i>Erolia a. alpina</i>	= <i>umbrinus</i> (Burm.) s. l.
† <i>incisus</i> (Piaget, 1880)	" <i>Phaeton flavirostris</i> " Error	Host probably <i>Anous stolidus</i> .
* <i>kilauensis</i> (Kellogg & Chapman, 1902)	<i>Heteroscelus incana</i>	p. 224.
* <i>lacustris</i> sp. n.	<i>Catoptrophorus semipalmatus inornatus</i>	p. 220.
<i>lari</i> (Packard, 1870)	<i>Larus marinus</i>	= <i>piceus</i> (Denny) s. l. (p. 201).
† <i>laveni</i> Eichler, 1953	<i>Charadrius h. hiaticula</i>	= <i>ochraceus</i> Nitzsch s. l.
* <i>limarius</i> sp. n.	<i>Limnodromus griseus scolopaceus</i>	p. 222.
† <i>limosae</i> (Kellogg, 1908)	<i>Limosa l. lapponica</i>	p. 224.
† <i>lyallpurensis</i> Ansari, 1955	<i>Tringa ochropus</i>	p. 217.
† <i>maurus</i> (Nitzsch, 1866)	<i>Chlidonias n. nigra</i>	= <i>piceus</i> (Denny).
* <i>mexicanus</i> Emerson, 1953	<i>Himantopus h. mexicanus</i>	p. 208.
† <i>milleri</i> (Kellogg & Kuwana, 1902)	<i>Anous stolidus galapagensis</i>	= <i>incisus</i> (Piaget).
† <i>morsitans</i> (Kellogg & Mann, 1912)	<i>Erolia melanotos</i>	= <i>umbrinus</i> (Burm.) s. l.
† <i>multisetosus</i> Blagoveshtchensky, 1940	<i>Lymnocyrtus minima</i>	

Species	Type Host	Comments
† <i>numenii</i> Rudow, 1866	. <i>Numenius arquata orientalis</i>	. = <i>patellatum</i> (Piaget) (see Clay & Hopkins, 1955 : 53).
<i>ocellatus</i> (Rudow, 1869)	. <i>Numenius p. phaeopus</i>	
† <i>ochraceus</i> (Nitzsch, 1818)	. <i>Pluvialis apricaria oreophilos</i>	. p. 203.
* <i>pacificus</i> (Timmermann, 1955)	. <i>Puffinus pacificus</i> Error ?	. Probably = <i>incisus</i> Piaget ; host : <i>Anous</i> sp. (p. 202).
<i>paetulus</i> (Kellogg & Kuwana, 1901)	. <i>Arenaria i. interpres</i>	. p. 233.
* <i>paludosus</i> sp. n.	. <i>Tringa nebularia</i>	. p. 219.
* <i>patellatus</i> (Piaget, 1890)	. <i>Numenius a. arquatus</i>	. p. 192.
† <i>pauliani</i> Séguy, 1954	. <i>Chionis minor</i>	. p. 203.
† <i>pediculoides</i> (Mjöberg, 1910)	. <i>Arenaria interpres</i>	. p. 191.
* <i>perplanus</i> (Kellogg & Chapman, 1899)	. " <i>Lunda cirrhata</i> " Error	. = <i>ochraceus</i> (Nitzsch), s. l. (p. 232).
† <i>perrarus</i> Blagoveshtchensky, 1948	. <i>Charadrius dubius coronicus</i>	. = <i>ochraceus</i> (Nitzsch), s. l.
* <i>piceus</i> (Denny, 1842)	. <i>Thalasseus s. sandvicensis</i>	
* <i>pustulatus</i> (Piaget, 1880)	. " <i>Gypogeranus (Spizaetus) cirratus</i> " Error	. = <i>spinulosum</i> (Piaget).
* <i>pustulosus</i> (Piaget, 1880)	. <i>Philomachus pugnax</i>	. p. 212.
† <i>raviensis</i> Ansari, 1955	. <i>Himantopus himantopus</i>	. = <i>himantopi</i> Blagoveshtchensky (p. 236).
* <i>sabulosus</i> sp. n.	. <i>Charadrius hiaticula semipalmatus</i>	. p. 228.
<i>scopularius</i> (Neumann, 1912)	. " <i>Passer domesticus</i> " Error	. ? = <i>gracile</i> (Piaget) (p. 236).
† <i>sedes</i> Eichler, 1944	. <i>Glareola p. pratincola</i>	. p. 196.
* <i>spinulosus</i> (Piaget, 1880)	. <i>Limosa l. limosa</i>	. p. 224.
<i>stictus</i> (Kellogg & Paine, 1911)	. <i>Capella delicata</i>	
<i>subpustulatus</i> (Carraker, 1910)	. " <i>Ceryle alcyon</i> " Error	. p. 235.
* <i>sulcatus</i> (Piaget, 1880)	. <i>Chlidonias n. nigra</i>	. = <i>piceus</i> (Denny).
<i>svobodai</i> (Balát, 1953) (corrected from <i>svobodae</i> by Balát, 1957)	. <i>Vanellus vanellus</i>	. = <i>gracile</i> (Piaget).
* <i>tetracis</i> sp. n.	. <i>Burhinus o. oedicnemus</i>	. p. 206.
* <i>tigrus</i> (Kellogg & Mann, 1912)	. <i>Arenaria melanocephala</i>	. = <i>bicolor</i> (Piaget) (p. 236).
* <i>timidus</i> (Kellogg, 1896)	. <i>Pluvialis d. dominica</i>	. = <i>ochraceus</i> (Nitzsch).
† <i>totani</i> (Schränk, 1803)	. <i>Tringa t. totanus</i>	. p. 215.
† <i>trilobatus</i> (Giebel, 1874)	. <i>Erolia minuta</i>	. = <i>umbrinus</i> (Burm.) s. l.
† <i>umbrinus</i> (Burmeister, 1838)	. <i>Erolia testacea</i>	. p. 212.
* <i>umbrinus</i> (Piaget, 1880)	. <i>Erolia testacea</i>	. = <i>umbrinus</i> (Burm.) (p. 214).
* <i>umbrosus</i> (Harrison, 1916)	. <i>Erolia testacea</i>	. = <i>umbrinus</i> (Burm.) (p. 212).
* <i>uniformis</i> (Kellogg, 1896)	. <i>Recurvirostra americana</i>	. = <i>uniseriatum</i> (Piaget) (p. 210).
* <i>uniseriatus</i> (Piaget, 1880)	. <i>Recurvirostra avosetta</i>	. p. 208.

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PLATE 4

- FIG. 1. *Actornithophilus crinitus* sp. n. Holotype. (Neg. no. 28330).
- FIG. 2. *Actornithophilus tetracis* sp. n. Holotype. (Neg. no. 28333).
- FIG. 3. *Actornithophilus sabulosus* sp. n. Holotype. (Neg. no. 27445).
- FIG. 4. *Actornithophilus sedes* Eichler. (Neg. no. 28325).
- FIG. 5. *Actornithophilus flumineus* sp. n. Holotype. (Neg. no. 28331).
- FIG. 6. *Actornithophilus kilauensis* (Kellogg & Chapman), ♀ lectotype.

